The Physical Oceanography of Bute Inlet, British Columbia[1,2]

By Susumu Tabata[3] and George L. Pickard[4]

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

Distributions of salinity, temperature, and oxygen of Bute Inlet based on twelve oceanographic surveys between the period August 1950 to July 1953 have been examined. The salinity structures of the shallow water during the various seasons can be classified under two main groups, one occurring at periods of small river runoff and the other at periods of large river runoff. In general, the surface salinity increases to seaward and with depth during all seasons. The surface water along the western shore is almost always observed to be less saline than along the eastern shore. The salinity of the deep water is 30.6 to 30.8‰ during both periods. The seasonal fluctuation of salinity at the surface is well marked but below a depth of 60 feet no obvious cycle exists. The temperature distributions can be divided into two main groups, winter and summer. During both seasons the surface temperature generally increases to seaward. The temperature gradient in the upper layers during the winter is positive (increasing vertically downward) and during the summer is negative (decreasing vertically downward). From early spring to late autumn, a well-defined temperature minimum, in the middle and upper reaches of the inlet, is evident in the intermediate depths. The water in the greater depths has a temperature of 8.0 to 8.2° C. and remains almost unchanged throughout the seasons. A seasonal temperature variation is observed down to a depth of 150 feet and is in phase with the air temperature cycle, but below this it is less noticeable. Insolation and cold runoff water from the rivers are predominant factors in determining the fluctuation in the sea temperature. The concentration of dissolved oxygen is usually high in the surface layer. The water at the greater depth is not stagnant as evidenced by the oxygen concentration.

Values from 0.2 to 1.5 g./cm./sec. for the eddy coefficient of conductivity have been determined for the intermediate depths.

I. INTRODUCTION

The first intensive study of a British Columbia inlet was that made by Tully (1949) of Alberni Inlet in the west coast of Vancouver Island. Subsequently, studies have been made of a number of the inlets in the mainland coast, and in particular both the Fisheries Research Board of Canada, Pacific Oceanographic Group, Nanaimo, and the Institute of Oceanography of the University of British Columbia have made observations of Bute Inlet. This is a deep narrow inlet which may be classed as an estuary in the sense that the fresh water in it is measurably diluted by sea water (Pritchard, 1952). The observations were made in part to provide background information and tests for theoretical studies of the circulation in such bodies of water (e.g., Cameron, 1951; Stommel, 1951).

[1]Received for publication September 17, 1956.

[2]Based on a thesis accepted by the University of British Columbia in partial fulfilment of the requirements for the degree of Master of Arts.

[3]Author's present address: c/o Fisheries Research Board of Canada, Pacific Oceanographic Group, Nanaimo, B.C.

[4]Author's present address: c/o Institute of Oceanography, University of British Columbia, Vancouver, B.C.

J. Fish. Res. Bd. Canada, 14(4), pp. 487–520, 1957.
Printed in Canada.

The series of observations for Bute Inlet are more extensive than for any other mainland inlets (twelve cruises during 1950–1953), and since it appears to be fairly typical in its characteristics, the following description of the water structure is presented.

II. GENERAL CHARACTER OF THE REGION

Physiography

Bute Inlet is a deep inlet, situated about 100 nautical miles northwest of Vancouver, British Columbia. The general features of this inlet and its adjacent regions are shown in Fig. 1. Like the other inlets of British Columbia and Southern Alaska, it represents a pre-glacial valley which has been subsequently modified by glacial erosion (Bancroft, 1913).

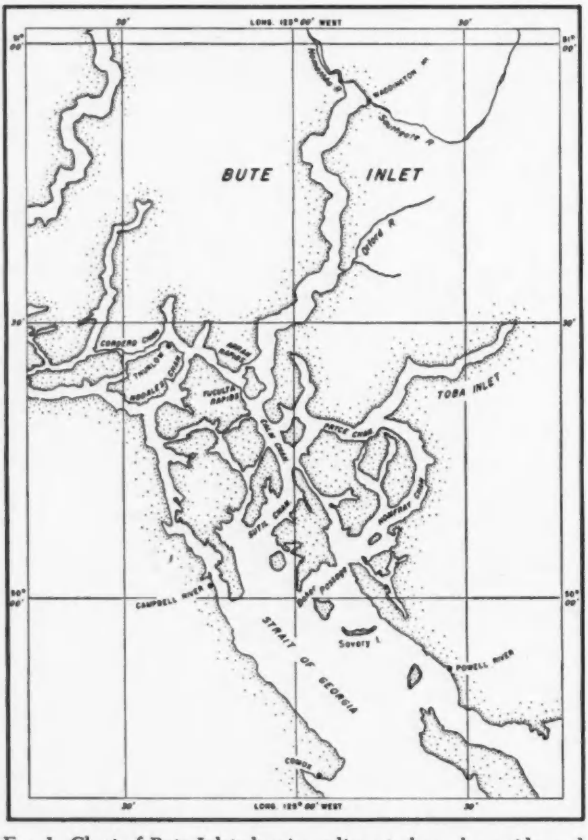


Fig. 1. Chart of Bute Inlet showing adjacent channels, rapids, and rivers.

From its head, which is fronted by silty mud banks, the inlet extends seaward in three reaches for 40 nautical miles. The width varies from 1¼ to 2½ nautical miles.

The sides are precipitous and rocky, with rugged mountains as high as 8,000 feet rising abruptly from the water. The higher summits are usually snow-capped all year round, and in the upper reaches of the inlet glaciers and patches of ice occupy the hollows of some of the lofty mountains.

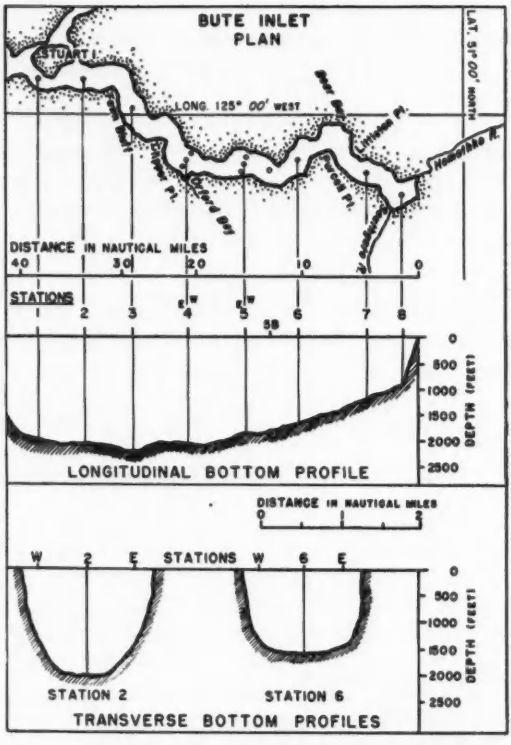


FIG. 2. Plan of Bute Inlet showing station positions and longitudinal and transverse bottom profiles.

The mountain slopes are as steep below the sea level as they are above, and the inlet still possesses the U-shaped cross sections (Fig. 2) which are similar to those of the large land valleys within this district. The bottom consists chiefly of fine grey mud of glacial origin, and appears to be level and smooth except near the head where considerable variations in depth occur. From the mouth, regarded as the region in the vicinity of Stuart Island (Fig. 2), the depth increases from 2,000 feet to a maximum of 2,200 feet at Station 3, between Fawn Bluff and Clipper Point, and then decreases toward the head.

The waters of Bute Inlet are in contact at its mouth with the well-mixed waters of Nodales and Cordero Channels through Yuculta and Arran Rapids, and also with the waters of the Strait of Georgia through Calm Channel and Pryce to Homfray Channels (Fig. 1).

Drainage

At the head of Bute Inlet are two rivers, the Homathko emptying into it from the north, and the Southgate from the east (Fig. 1). The former has its headwater in the interior plateau of British Columbia and flows through the Coast Range, where it is joined by many tributaries arising from glaciers. The Southgate, on the other hand, has less contribution from such tributaries. Midway along the inlet another but smaller river, the Orford, enters the inlet. Besides these principal rivers, the inlet receives many cascading streams which are dry or negligible in August and September, but are well developed during the heavy precipitation of winter, and especially in late spring and early summer when the stored winter snow at higher levels is melting. It is the quantity of the freshwater discharge (runoff) into the inlet which gives it the character of an estuary.

III. COLLECTION AND TREATMENT OF DATA

Data were available from twelve separate oceanographic surveys between the period August 1950 to July 1953, inclusive. The first five surveys were conducted by the Pacific Oceanographic Group and the remainder by the Institute of Oceanography. A catalogue of the surveys is shown in Table I.

Table I. Catalogue of the surveys during the period August, 1950 to July, 1953 showing cruise details.

Cruise No.	Cruise date From	To	Number of hydrographic stations	Authority
I	2 Aug. 50		2	P O G*
II	10 Sept. 50		7	P O G
III	28 Nov. 50	– 30 Nov. 50	18	P O G
IV	11 Jan. 51		6	P O G
V	20 Feb. 51	– 22 Feb. 51	22	P O G
51-2-I	17 May 51	– 26 May 51	44	I O U B C†
51-2-II	4 Aug. 51		4	I O U B C
51-3	25 Oct. 51	– 26 Oct. 51	13	I O U B C
52-1	30 Mar. 52	– 31 Mar. 52	3	I O U B C
52-2	29 May 52	– 11 June 52	3	I O U B C
52-3	9 Aug. 52	– 13 Aug. 52	14	I O U B C
53-4	30 June 53	– 9 July 53	23	I O U B C

*Fisheries Research Board of Canada, Pacific Oceanographic Group, Nanaimo, B.C.
†Institute of Oceanography, University of British Columbia, Vancouver, B.C.

Collection of Data

Surface water samples were obtained by using an ordinary bucket while all subsurface samples were collected by Atlas, Nansen, Ekman or Fjarlie water sampling bottles secured to a hydrographic wire at the desired intervals.

The sea surface temperatures were obtained by a chemical thermometer immersed in a sample of water drawn from the surface in a bucket. Subsurface temperatures were obtained by reversing thermometers attached to sampling bottles and also by bathythermographs. Temperatures from the reversing thermometers were also used to calibrate and check the bathythermograph readings.

Measurements for both the salinity and dissolved oxygen were made by conventional titrations, the former using the Mohr method and the latter using the Winkler method.

The oxygen content of the water is expressed as a percentage of saturation solubility (percentage saturation) at the temperature and salinity in situ.

Treatment of Data

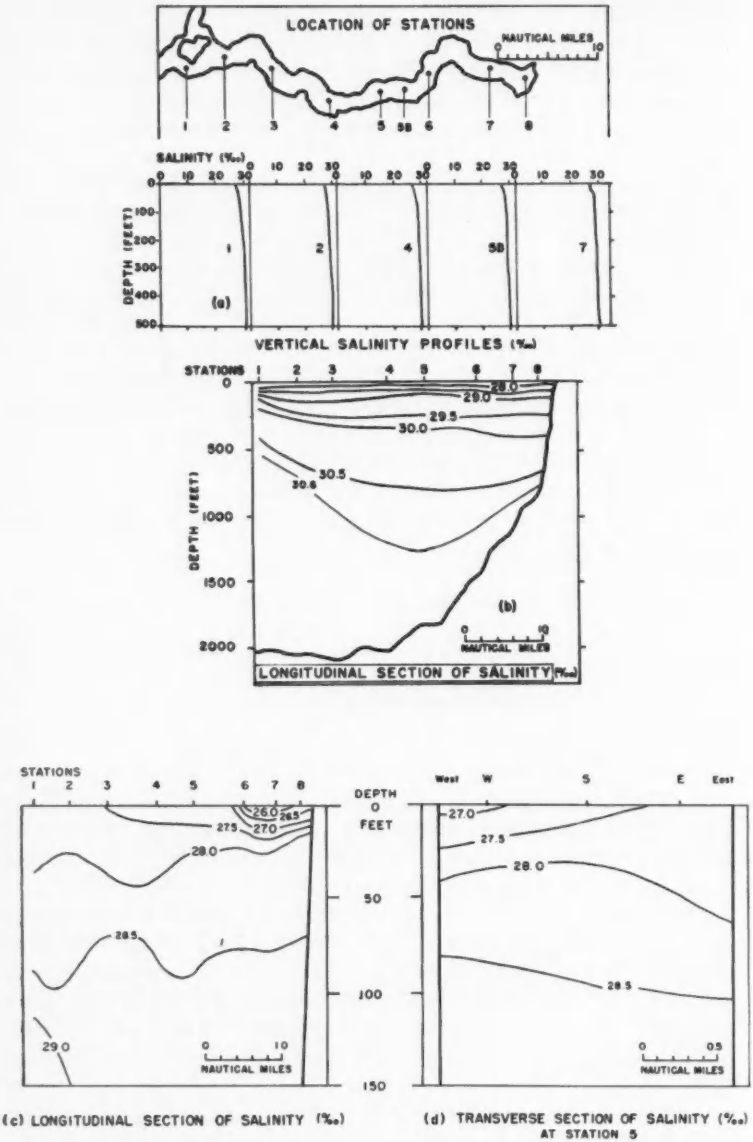
The salinity, temperature, oxygen saturation, and density anomaly (σ_t) data from each station were plotted as functions of depth, and temperature–salinity (T–S) diagrams were constructed. (σ_t is defined by $(1 - \rho_t)10^3$, where ρ_t is the density anomaly of a sea water sample at the temperature at which it was collected.) For each cruise, longitudinal and transverse sections of salinity, temperature, and density were drawn, with additional sections to show the details above the depth of 150 feet.

IV. General Characteristics of the Water Structure

The general characteristics of the salinity, temperature, density anomaly (σ_t), and oxygen distributions will be presented first, and the details of the structure and temporal variations discussed subsequently.

Salinity

The salinity distributions for the different seasons may be classified under two main groups, one occurring at periods of small river runoff (October to April) and the other at periods of large river runoff (May to September). During the small runoff period the difference in salinity between head and mouth is about 3‰, while during the large runoff period it may be as large as 20‰. These differences are the same as the differences between the surface and the deep water in mid-inlet during the same periods. Profiles for periods of small and large runoff are shown in Fig. 3a and 4a respectively. As illustrated in these Figures, the salinity gradients are smaller during the low runoff period than during the large runoff period. Typical salinity distributions for the period of small runoff are shown in Fig. 3b, c, and d, and for the periods of large runoff in Fig. 4b, c, and d. The regular slopes of the isohalines in the shallower depths during large runoff (Fig. 4c) illustrate the gradual mixing of the fresh and sea water as the former progresses down the inlet. As shown in the transverse sections for both periods (Fig. 3d and 4d) the surface water along the western shore of the inlet is less saline than along the eastern shore. The deep water during both periods has a salinity of 30.6 to 30.8‰, which remains substantially unchanged throughout the season in contrast to the wide variations which occur in the upper layers.



(c) LONGITUDINAL SECTION OF SALINITY (‰)

(d) TRANSVERSE SECTION OF SALINITY (‰) AT STATION 5

FIG. 3. Salinity of water in Bute Inlet during small runoff period (Winter).

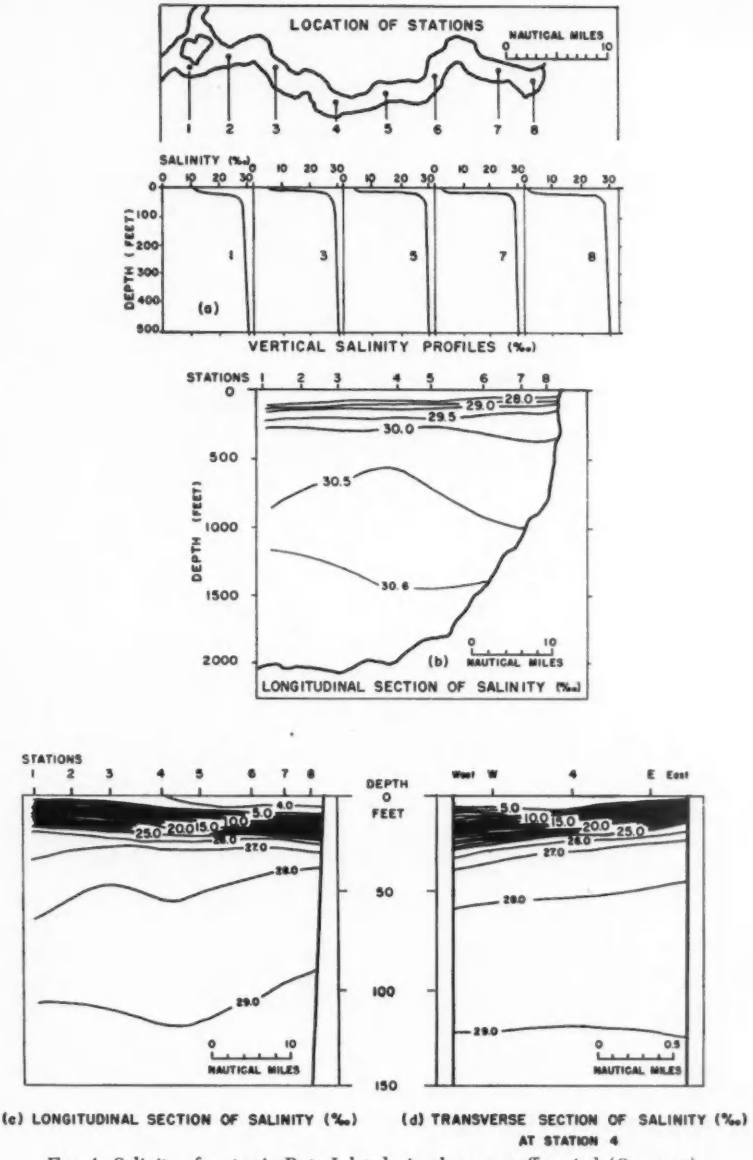


FIG. 4. Salinity of water in Bute Inlet during large runoff period (Summer).

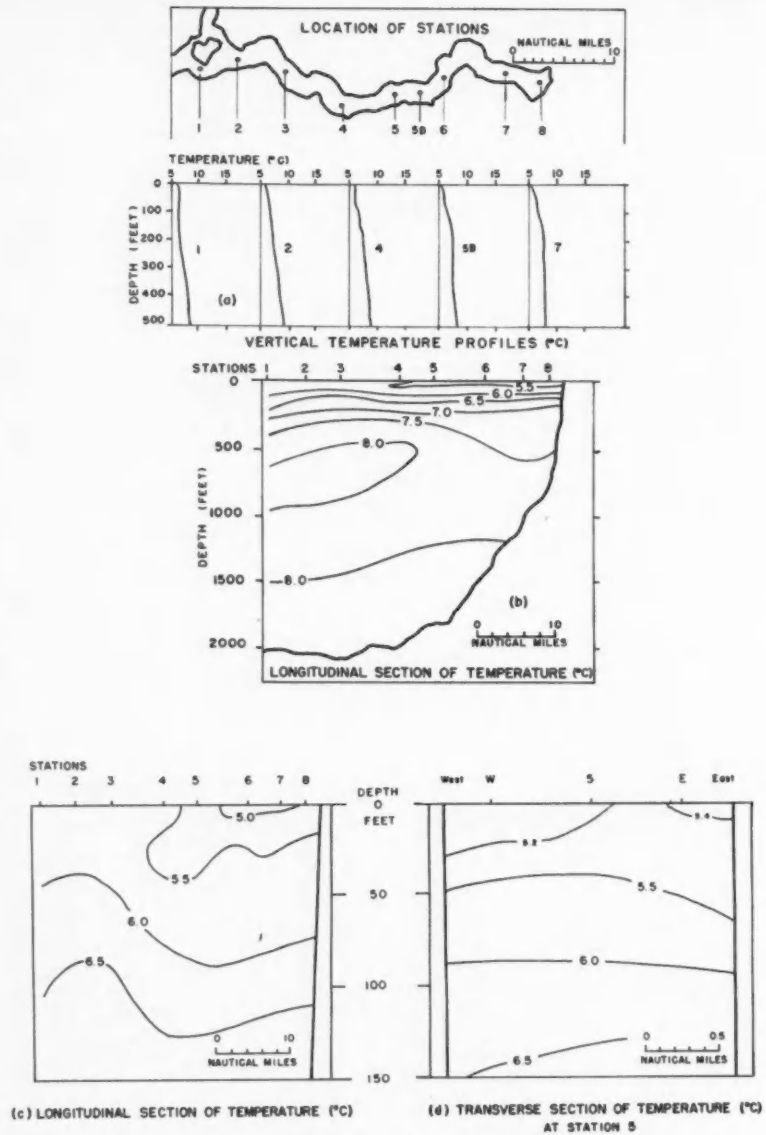


FIG. 5. Temperature of water in Bute Inlet during Winter.

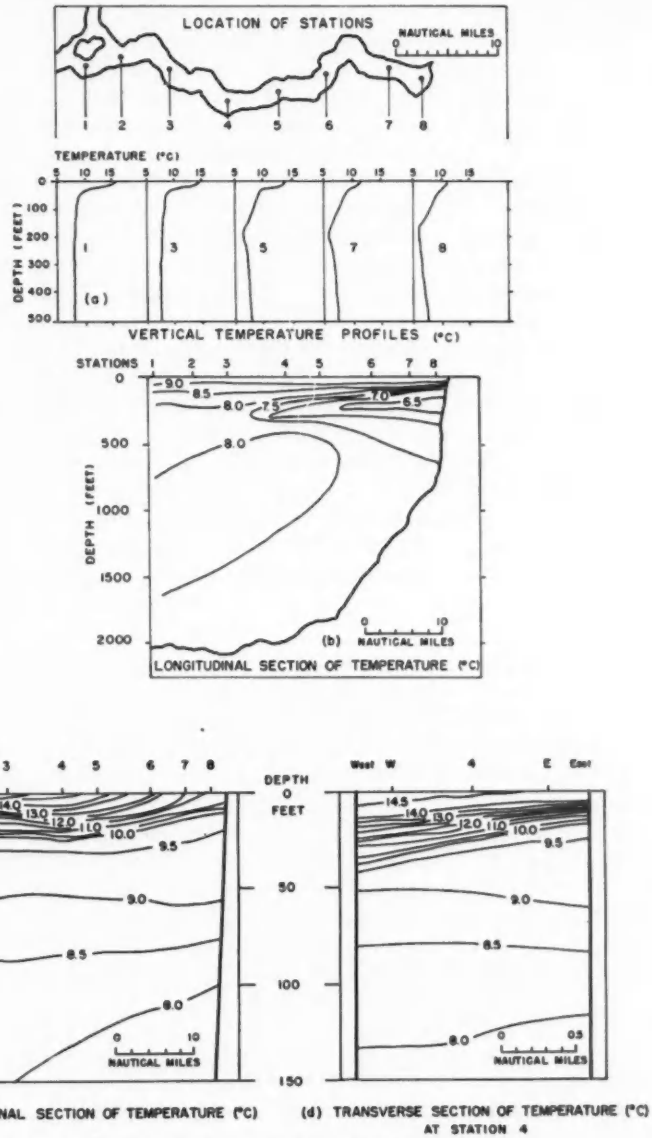


FIG. 6. Temperature of water in Bute Inlet during Summer.

Temperature

The temperature distributions may be divided into two classes, winter and summer. As illustrated in Fig. 5a and 6a, the temperature profiles for the upper 500 feet for both periods are less regular than those of the salinity (Fig. 3a and 4a). The less simple pattern in the temperature distributions as compared to that of the salinity is again evident in the longitudinal sections (Fig. 5b and 6b) although the transverse distributions of both the salinity and temperature in the upper 150 feet are of the same character (compare Fig. 3d with 5d, and Fig. 4d with 6d). In general, the temperature in the upper layer and also at the intermediate depths increases progressively from the head seaward (Fig. 5c and 6c). During the winter the temperature increases with depth to a maximum at a depth of several hundred feet and then decreases gradually to the bottom. The vertical temperature gradients in the upper water during this period are smaller than those during the summer (Fig. 5a and 6a). During the summer, the temperature all along the inlet, except at the mouth, decreases with depth to a well-defined minimum at a depth of 200 to 300 feet, then increases to a maximum at 800 to 1,000 feet, similar to that evident during the winter, and finally decreases slowly to the bottom (Fig. 6a). The salient feature of the seasonal temperature variation is that it is in phase with the air temperature variation. It is large at the surface and evident to depths of 150 or even 300 feet. Below this depth, the temperature remains almost constant at 8.0 to 8.2° C. throughout the year.

Oxygen

In general, the concentrations of dissolved oxygen, expressed as percentage saturation, are very high in the surface layer, with maxima of 90% to 130% occurring near the halocline but not necessarily coinciding with it. As shown in Fig. 7, the concentration drops from the above maxima to 80% in the winter and 70% in the summer at a depth of 60 feet, and from this depth it decreases gradually to 50 to 35% in the deeper water. The high oxygen values above 100% in the surface layer away from the head are associated with phytoplankton blooms (Gran and Thompson, 1931). In the summer months such values are higher than in the winter months, due primarily to the seasonal increase in plankton activity. Since the concentration of oxygen in the deeper water of Bute Inlet is not low it may be presumed that an inflow of water must be present to maintain this oxygen level.

Density Anomaly (σ_t)

The density anomaly (σ_t) curves for the water of this inlet generally follow those of the salinity more closely than those of the temperature, as illustrated in Fig. 8. Consequently, the comments on salinity will apply except in special cases. Longitudinal sections of density anomaly for winter and summer are shown in Fig. 9; these may be compared with those of salinity (see Fig. 3b and 4b) and contrasted with those of temperature (see Fig. 5b and 6b). During both periods, the density anomaly of the deep water has values between 23.8 and 23.9.

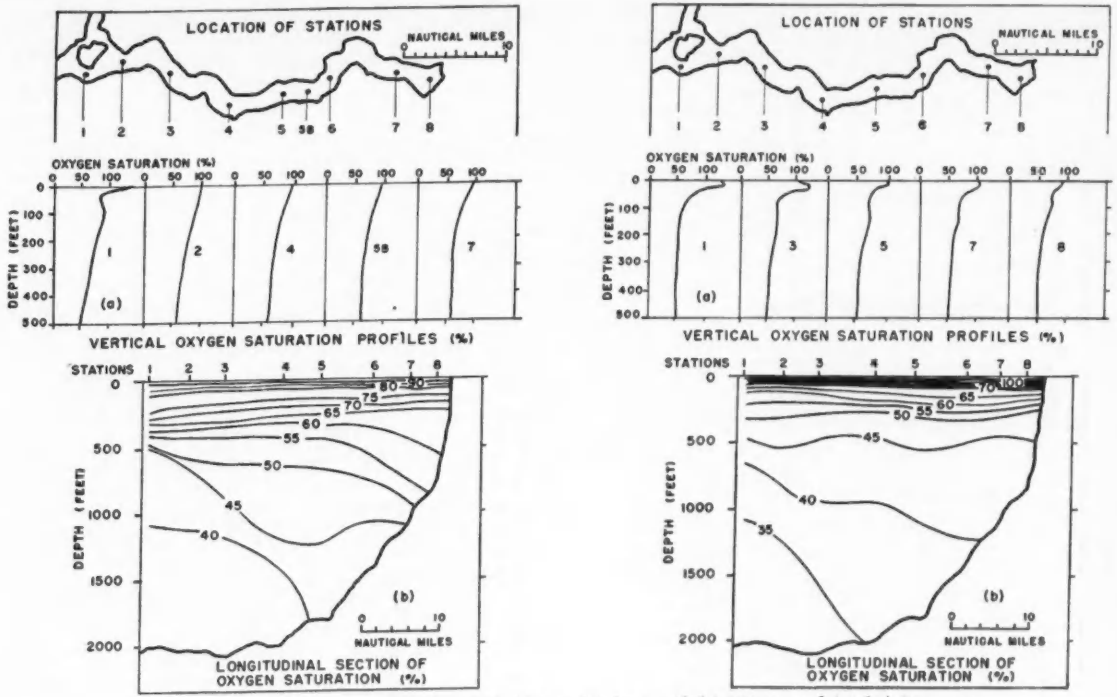


FIG. 7. Dissolved oxygen content of water in Bute Inlet during (left) Winter and (right) Summer.

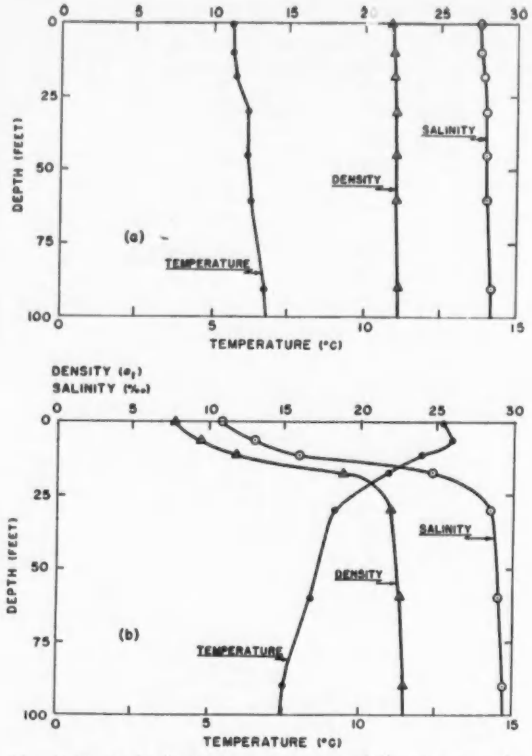


FIG. 8. Typical salinity, temperature, and density anomaly (σ_t) profiles for Bute Inlet during (a) Winter and (b) Summer, illustrating the similarity between the salinity and density anomaly profiles.

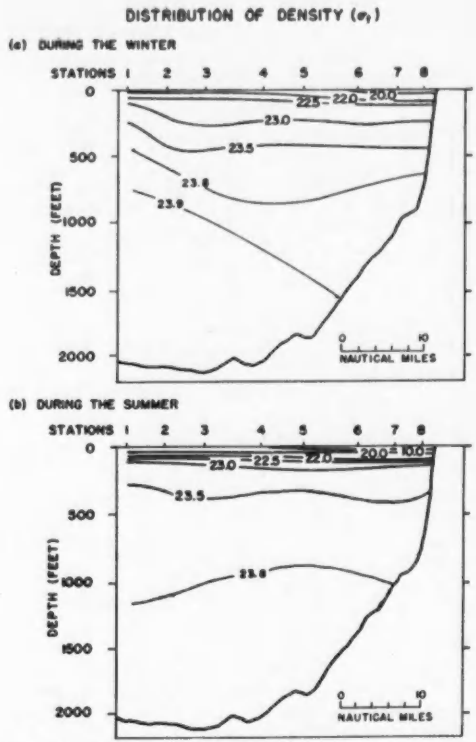


FIG. 9. Vertical sections showing distribution of density anomaly (σ_t) of water of Bute Inlet during (a) Winter and (b) Summer.

V. DETAILS OF THE WATER STRUCTURE

An examination of the T–S diagrams for the waters in the inlet suggests that three main water masses may be identified. These masses are indicated in Fig. 10 and are designated as follows:

Winter Surface Water (W), with temperature of 5 to 6° C. and salinity of 27 to 29‰,

Runoff Water (R), with temperature of 6 to 7° C. and very low salinity, and

Deep Water (D), with temperature of 7.5 to 8.5° C. and salinity of 30.5 to 30.8‰.

(For convenience the water lying between the deep water and the mixed runoff water will be named Intermediate Water.)

The water masses of Nodales Channel (N) and Strait of Georgia (G) (below a depth of 60 feet) are also shown.

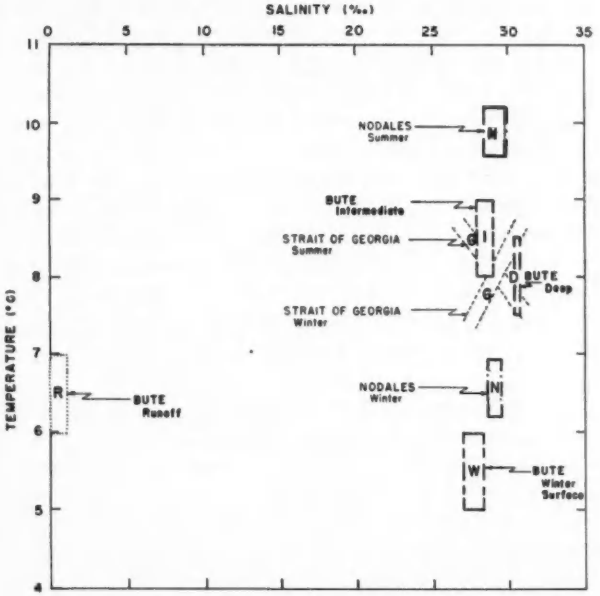


FIG. 10. Temperature–salinity relations in Bute Inlet, Nodales Channel, and Strait of Georgia, illustrating the various water masses.

For the purpose of describing the structures of the waters of Bute Inlet, the study of the data has suggested the following defined divisions: Winter (December, January, and February), Spring (March, April, and May), Summer (June, July, and August), Autumn (September, October, and November). March and September may be considered as transitional periods. With this introduction, the seasonal distribution of salinity and temperature will now be discussed season by season.

Winter

During the Winter the runoff from river drainage is low (Fig. 19) and consequently the salinity of the surface water of the inlet reaches a relatively high value along most of its length (Fig. 3c). The fact that the lowest winter salinity observed near the head was 18.4‰ (January 1951) indicates that what little volume of fresh water enters the inlet soon undergoes mixing with the more saline water of the inlet. This mixed water at the head occurs in the upper zone whose boundary can be located from the halocline (usually accompanied by the thermocline) at about 5 feet. By February, the water in the upper 20 to 30 feet reaches near homogeneity. Associated with this the boundary of the upper zone generally occurs at about 20 feet in the upper reaches of the inlet and reaches about 30 feet at mid-inlet, becoming less evident toward the mouth. Water of salinity lower than that at the head has been observed at Station 7, several miles from the head; such occurrence is probably due to the eddies formed by the surface current or from a cloud of fresh water trapped by tidal movement of saline water. Along the western shore the surface water is observed to be less saline than along the eastern side. Associated with this, the transverse isohalines, as shown in Fig. 3d, slope downward from the east to the western shore. This fact is attributed to the effect of Coriolis force.

The air temperature also reaches a minimum during the Winter (see Fig. 20) and consequently the sea surface temperature is expected to be low at this time. (This does not imply that the air temperature is the only factor controlling the sea temperature.) Pickard and McLeod (1953) have established that there is a strong correlation between the long-term averages of the air and sea surface temperatures, especially in the sheltered regions of the coast such as the Strait of Georgia. Since Bute Inlet is also in a sheltered area, this relation is presumed to be true here.

Owing to the cold air mass over the inlet, the surface water is cooled and during January a minimum sea surface temperature (4° C.) is reached. As illustrated in Fig. 5d, the surface temperature along the inlet is generally around 5° C. in the upper reaches and 6° C. in the lower reaches of the inlet. Because of the relatively warm December of 1950 (monthly mean air temperature 5° C.) the subsurface water below the depth of 10 feet did not cool as much as usual and remained almost unchanged from November to January. However, between January and February there was a general drop in temperature (from 0.5 to 1.0 degree) in the subsurface waters and even at a depth of 150 feet the temperature dropped by 0.5 degree, from 7.3° to 6.8° C., during this interval. The relation between air and sea temperature is discussed in detail later.

In January and February as the runoff approaches the minimum, and as the water near the surface is cooled under the influence of the cold northerly wind that has been observed in this inlet during the Winter, an almost homogeneous water is formed which is presumed to be the consequence of wind mixing. A distinct water mass of salinity 27 to 28‰ and temperature of 5 to 6° C. forms in the upper 20 or 30 feet. This is designated as Winter Surface Water (Fig. 11). During the winter months strong offshore gales called "Squamishes" frequently

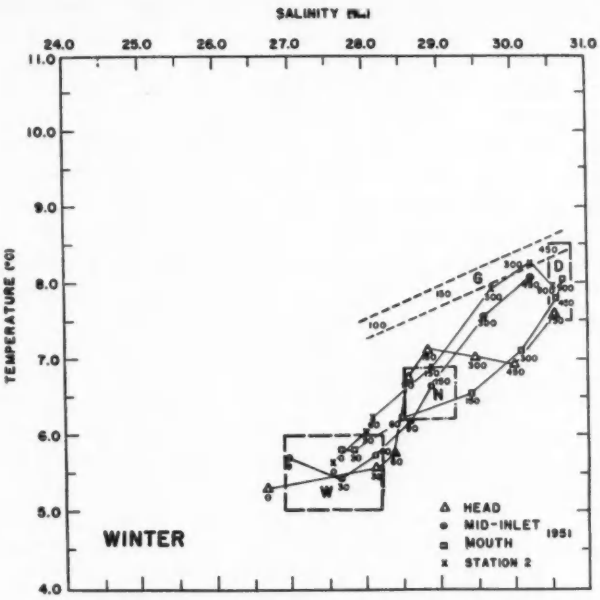


FIG. 11. Temperature–salinity relations in Bute Inlet for Winter period (depths in feet).

occur in the British Columbia inlets (Tyner, 1950). These winds are usually associated with the presence of the cold Arctic air mass over the province of British Columbia and therefore would be influential in cooling the inlet waters mainly by evaporation. Depending on the severeness and persistence of such conditions, the Winter Surface Water may be colder and may extend to a greater depth.

The Deep Water has a salinity of 30.5 to 30.8‰ and a temperature of 7.5 to 8.5° C. with little or no seasonal variation. A tongue-like body of warm water with a maximum temperature of 8.3° C. occurs below 300 feet and above 1,000 feet depth and intrudes well into the inlet (Fig. 5b). The water at a depth below 300 feet is similar in salinity though colder than that of the water at similar depths in the northern part of the Strait of Georgia (Fig. 11). Whether this tongue of warm water can be identified with the intruding water from the Strait of Georgia or not is difficult to establish. At the present time, little is known of the process of the exchange of deep water but it may be possible that the deep water flows in over the sills from the Strait of Georgia to Bute Inlet (depths at Baker Passage and in the passage between Savary Island and the mainland are both about 450 feet). The well-mixed water coming through Yuculta and Arran Rapids is characteristically the same as that at a depth of 150 feet in Bute Inlet. Therefore it is unlikely that the water from these rapids supplies the water in the greater depths in Bute Inlet.

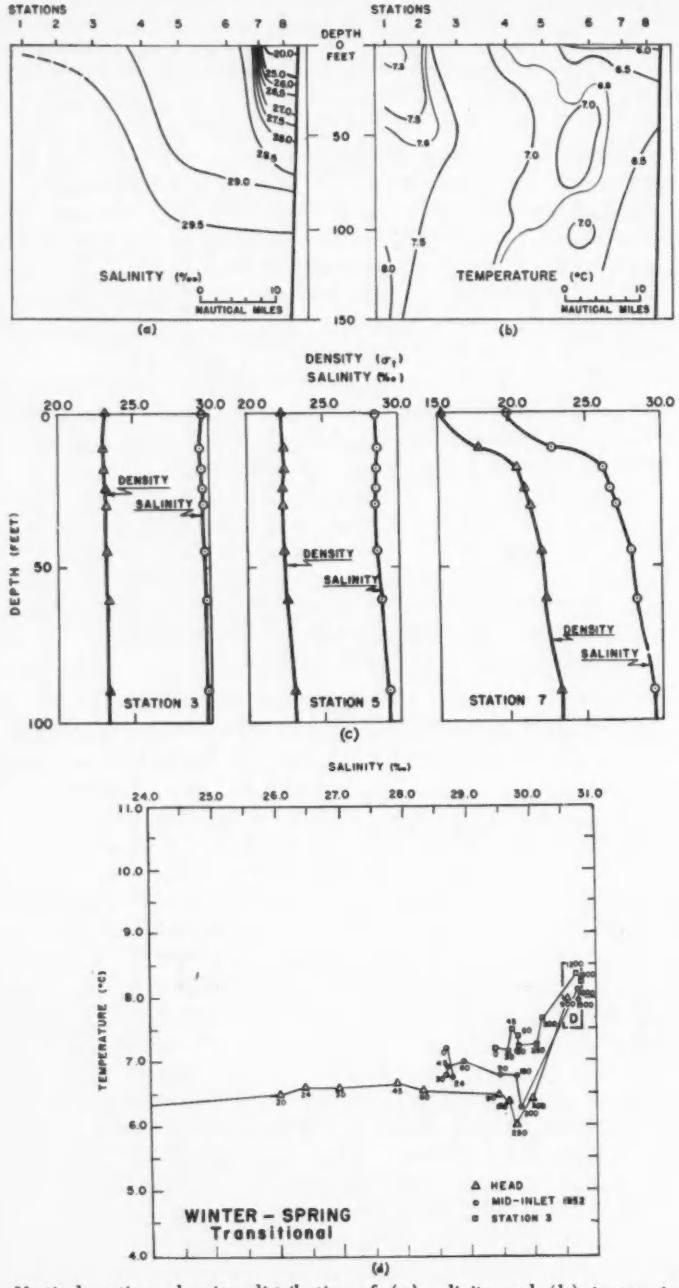


FIG. 12. Vertical sections showing distribution of (a) salinity and (b) temperature during Winter–Spring transitional period. (c) Typical salinity profiles and density anomaly (σ_t) profiles for Winter–Spring transitional period. (d) Temperature–salinity relations in Bute Inlet for Winter–Spring transitional period.

The cold surface water flows to seaward and as it progresses it mixes with the warmer and more saline water of the inlet as indicated by the increase in salinity and temperature towards the mouth. This surface flow is confirmed by current measurements with drift buoys which indicate a net seaward flow during the tidal cycle (Cruise V, February 1951). In order to compensate the salt transported out of the inlet through the upper layer a counter flow below this layer must be postulated to maintain the continuity. Tully (1949) has shown that in Alberni Inlet the mixing depth not only separates the upper and lower layers in in structural patterns, but also divides the current system. It appears that this is also true in the current system of Bute Inlet and it is presumed that the depth of no motion is close to the depth of the halocline.

Since the concentration of dissolved oxygen in the deeper water is relatively high (40% to 50% at 1,300 feet depth, see Fig. 7) it may be assumed that the water in the greater depth is not stagnant and thus a deep water circulation is likely to be present in this inlet.

In March 1952 the surface zone showed little evidence of fresh water in the upper layer, except near the head where an upper zone of relatively low salinity occurred as shown in Fig. 12a and 12b. Typical salinity and density anomaly (σ_t) profiles for this period are shown in Fig. 12c; it is readily seen that the water in the upper 50 feet is almost homogeneous except at the head. This period may be referred to as Winter–Spring Transitional.

The T–S diagrams for this period are shown in Fig. 12d in which a surface water that is slightly warmer (7° C.) and more saline (29.0‰) than that of February 1951 (Fig. 11) is evident in the upper layer. The minimum temperature layer can be recognized at depths of 250 to 300 feet and appears to have formed some time during the winter.

Spring

In a later section it is shown that there is good reason to conclude that the peak discharges of the Homathko and Southgate Rivers during 1951 and 1952 were reached in June and July respectively.

In the latter part of May and in the early part of June the runoff due to river discharge is close to or at a maximum level and therefore a large volume of fresh water is being transported into the inlet. This cold fresh water (temperature of about 7° C. and salinity less than 1‰) designated R (see Fig. 10), undergoes mixing with the warmer and more saline water and soon reaches a salinity greater than 1‰ and temperature greater than 8° C. The temperature increase must also be augmented by insolation and heat obtained from the atmosphere. The mixing results in the formation of an upper brackish layer which, in general, increases in salinity and temperature as it progresses seaward (Fig. 13a and 13b) This progressive mixing is illustrated in the set of salinity profiles shown in Fig. 4a. The mixing zone which is defined to be the zone lying between the upper brackish layer and the more saline lower layer, occurs on the average between the depths of 10 feet (upper limit) and 24 feet (lower limit) and appears to occupy the same depth along the inlet except near the mouth, where it is

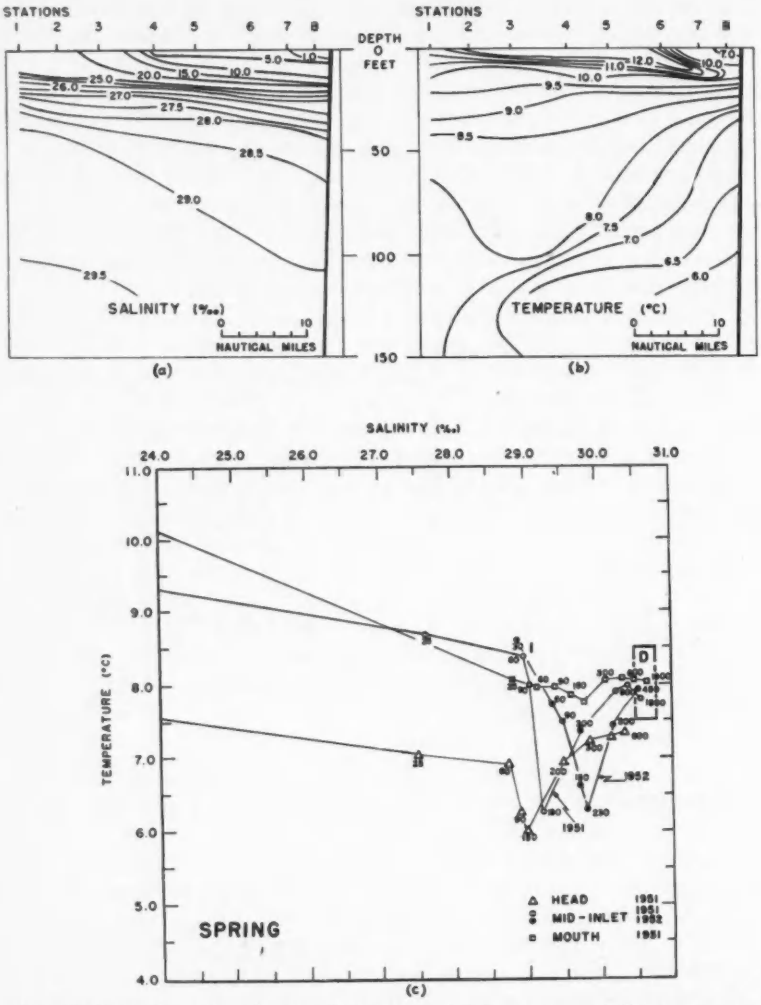


FIG. 13. Vertical sections showing distribution of (a) salinity and (b) temperature during Spring period. (c) Temperature–salinity relations in Bute Inlet for Spring period.

shallower. Tully has already remarked on the constancy of the depth of this zone at any particular time and at any particular stage of tide in Alberni Inlet (Tully, 1949) and it is believed this is also characteristic of Bute Inlet. The salinity structure below the mixing zone is not too different from that of the Winter period (compare Fig. 3c and 13a).

Since the Winter period there has been a substantial surface warming (from about 5 to 12° C.) due primarily to insolation and this is shown by the development of a thermocline in the shallower layer followed by a slower decrease to the minimum at intermediate depths.

The minimum-temperature layer remains at the same depth as it did in the Winter–Spring Transitional period and increases very little in temperature (0.2 to 0.3 degree). Obviously, the insolation has not influenced this layer much, nor has the warmer water below. Although the temperatures of the minimum-temperature layer of the two years 1951 and 1952 are the same, the average depth at which this layer occurs in 1951 is shallower by about 50 feet from that of 1952 (see Fig. 13c).

A tongue of warm water similar to that found during the Winter period is still evident in the greater depths (see Fig. 5b), but at this time has intruded farther into the inlet.

The T–S diagram for the mouth of the inlet is modified and this is believed to be the result of mixing with the waters from Yuculta Rapids, Arran Rapids, and Calm Channel.

The fresh water which is continually supplied at the head, and which subsequently mixes with the more saline water of the inlet, flows seaward in the upper zone. Current observations at mid-inlet often indicate a seaward flow in the upper zone during the entire tidal cycle, the velocities being larger during the ebb than during the flood. The fact that the brackish water is carried seaward indicates that some salt is transported out of the inlet in the upper zone. Assuming conservation of salt there must be a replenishment of salt for that lost through the upper zone. This replenishment is believed to occur in the middle zone and also possibly below this zone.

In view of the observation that the water on the western shore of the inlet has a lower salinity than that along the eastern side it is probable that more fresh water is transported out of the inlet along the western than along the eastern shore.

Since the minimum-temperature layer remains constant in depth and changes very little during the interval between the two periods, the net vertical motion near this layer must be very small.

Summer

During the Summer period a greater volume of fresh water is being discharged into the inlet than during the Spring period (see Fig. 19). The surface salinity is less than during the Spring period (compare Fig. 4c and 13a). It may be noted that the 10.0‰ isohaline reaches the mouth, whereas the same isohaline reaches only to mid-inlet during the Spring period. The upper zone in the summer of 1950 was deeper than in the succeeding summers. This is attributed to the fact that during the summer of 1950 the river discharge was much greater than that during the other summers. The salinity structure for the greater depths is again the same as that for the Spring period.

In phase with the air temperature which reaches a maximum in July or August, the surface temperature increases considerably (3 degrees) above that for the Spring period and reaches its annual maximum. The subsurface layer is also influenced by this heating as evidenced in the temperature pattern (compare Fig. 5c and 13b) which shows a general warming up of this layer to a depth of about 150 feet. The minimum temperature increases by about 0.5 degree during the intervening period. Below this depth the water remains almost constant in temperature during the interval between the Spring and Summer periods.

As shown in the T–S diagrams of Fig. 14, there is a modification in the structure of the water at the minimum-temperature layer, where both the temperature and salinity have increased moderately. From Fig. 14, it is evident that the water at the minimum-temperature layer is about 1.5 degrees colder in 1950 than in 1951 and 1952. This difference is attributed to the severe winter of 1949–1950 when the water at the minimum-temperature layer was formed. As illustrated in Fig. 14, the Deep Water of Bute Inlet is similar in character to that of the Strait of Georgia.

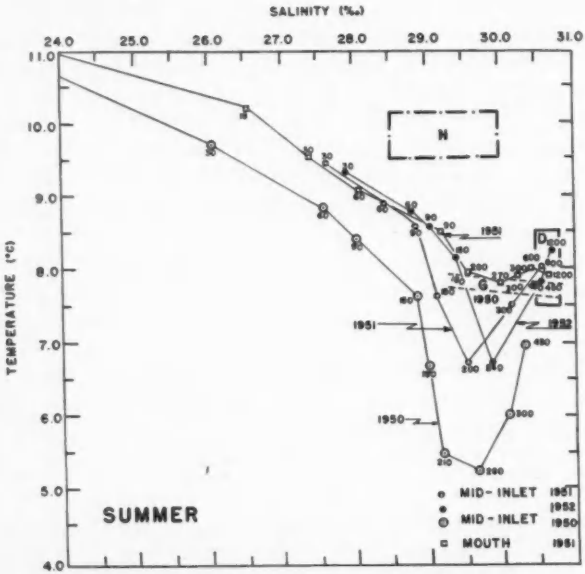


FIG. 14. Temperature–salinity relations in Bute Inlet for Summer period.

Conditions observed during September 1950 (Fig. 15) are indicative of the transition from summer to autumn. This period may be referred as Summer–Autumn Transitional. By this time the runoff is reduced to half the peak flow for the year, and is almost the same as that for the spring. Concurrently with this

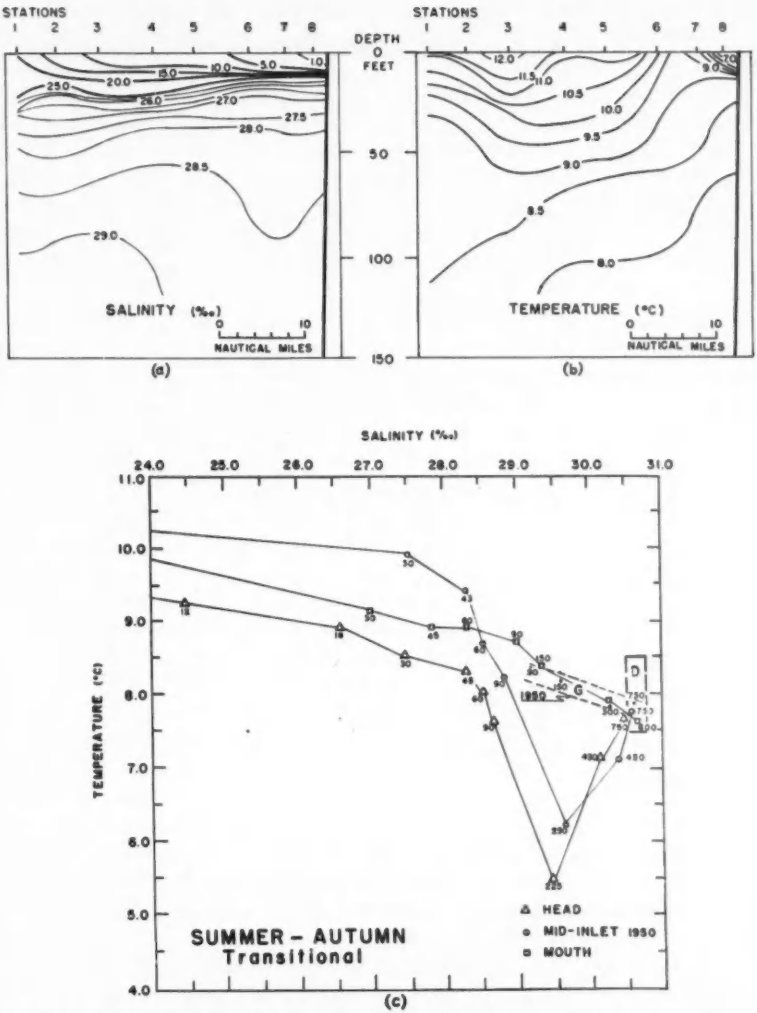


FIG. 15. Vertical sections showing distribution of (a) salinity and (b) temperature during Summer–Autumn transitional period. (c) Temperature–salinity relations in Bute Inlet for summer–autumn transitional period.

drop in the runoff, the air temperature drops by 2 to 3 degrees (C.) from the maximum attained during the summer, to the same value as that for the spring.

The conditions are therefore similar to those of the characteristic Spring patterns, both in the temperature and salinity structures as seen from the comparisons of the vertical sections of this period (Fig. 4c and 15a) with the cor-

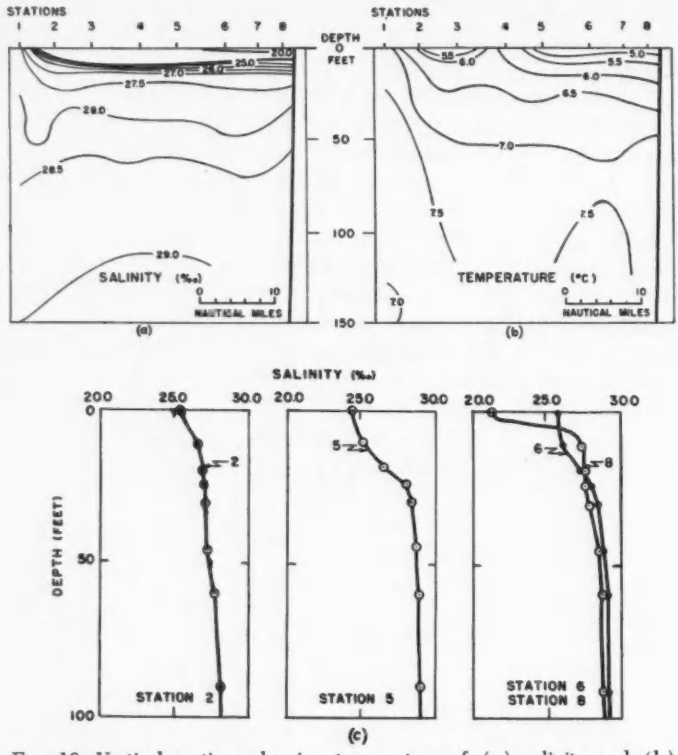


FIG. 16. Vertical sections showing temperature of (a) salinity and (b) temperature during Autumn period. (c) Typical salinity profiles for Autumn period.

responding sections for the Spring (Fig. 13a and 13b). The upper zone is seen to be shallower than during the summer, and in the upper 30 feet the temperature structure is the same as that for the spring, but below this it is identical with that for the summer. Apparently, the surface cooling has not yet penetrated beyond the depth of 30 feet. The T–S diagrams also indicate that the Intermediate Water has almost the same characteristics as during the Summer period.

The Deep Water has undergone no major changes since the Summer period. As seen by comparing Fig. 14 and 15c, the water at the minimum temperature layer has increased in temperature by 0.5 degree and increased in salinity by 0.3‰. The T–S relations for the water of the Strait of Georgia are included in Fig. 15c to show that the Deep Water in Bute Inlet is similar in character to that in the Strait of Georgia at this time of the year.

AUTUMN

In the autumn, the runoff due to river discharge decreases to a value which is

only twice the minimum discharge. At the same time, the air temperature decreases rapidly from a maximum value of 17° C. attained during the summer to about 6° C. at this time.

The salinity in the upper layer is much greater than during the preceding periods (Fig. 15a and 16a, 16c), and the structure is similar to that for the winter. During this period, the fresh water entering at the head is sufficient to form a well-defined layer only at the upper reaches of the inlet. Nearer to the mouth the mixing eliminates the sharp boundary between the upper and lower layers (Fig. 16c).

In the Deep Water, however, the salinity structure is the same as during the preceding period.

The decrease of about 7 degrees in the air temperature is accompanied by a decrease of 4 to 6 degrees in the temperature of the surface layer, but of less than 1 degree at a depth of 150 feet as compared with conditions at the end of the summer period (compare Fig. 15b with Fig. 16b). The water lying between the depths of 150 feet and 200 feet has been cooled and as a consequence cells of warm water are formed, sandwiched between the surface cold water and the cold water at the minimum-temperature layer (Fig. 17a). Thus a reversal in the temperature gradients has taken place (negative to positive) in the upper layer. On comparing the T–S diagrams for this period (Fig. 17b) with those for the preceding period, it is seen that the water at the minimum-temperature layer has increased in temperature by 0.6 to 0.8 degree from the preceding period.

The shallow transverse salinity structures again (as in winter) exhibit the isohaline sloping downward from the eastern to the western shore of the inlet except at Station 5.

The seasonal cycle of events is completed at this stage and from here, with further cooling and reduced runoff, a typical Winter scene again reappears.

Circulation

Very few direct observations of currents have been made in Bute Inlet, but these and the character of the salinity and temperature structures indicate that a typical estuarine circulation takes place in this inlet with outflow occurring in the upper layer and replenishment of saline water occurring below this. The net seaward transport increases from head to mouth, and is much higher during the maximum runoff period than at other times. Transit times from head to mouth of the order of 4 to 8 days have been estimated.

VI. SEASONAL VARIATION OF SALINITY AND TEMPERATURE

The seasonal fluctuation of temperature and salinity of the waters in the Strait of Georgia has been studied by Hutchinson, Lucas and McPhail (1929), and more recently the seasonal variation of temperature and salinity of the surface waters of the British Columbia coast has been analysed by Pickard and McLeod (1953). On the Atlantic coast similar studies have been made by Hachey (1939), Hachey and McLellan (1948) and recently by Lauzier (1957).

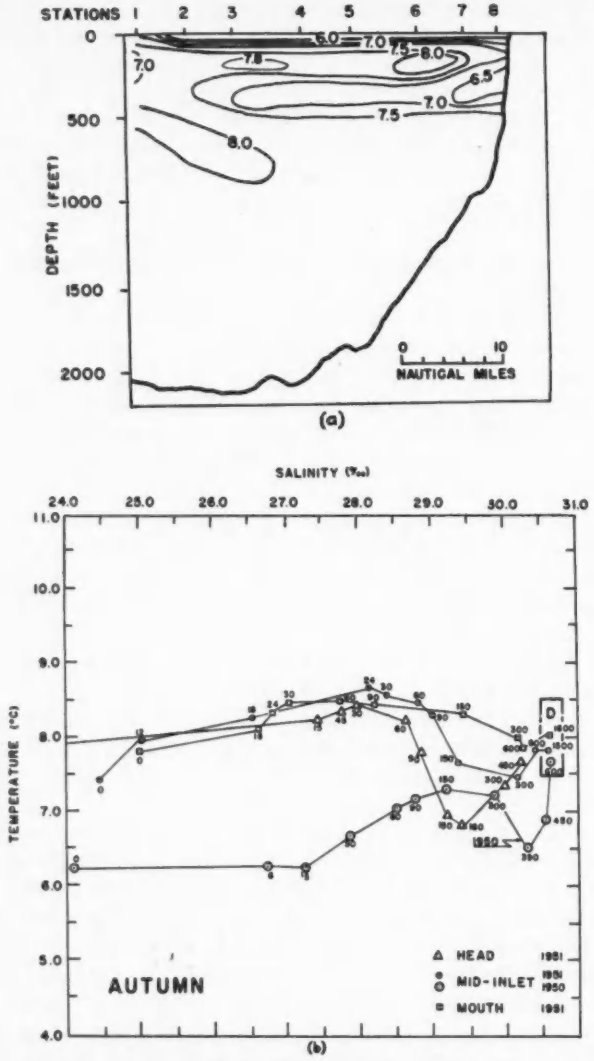


FIG. 17. (a) Vertical sections showing temperature during Autumn period. (b) Temperature–salinity relations in Bute Inlet for Autumn period.

Most of the above studies were based on consistent data which were collected regularly. The data available for Bute Inlet are irregular, but an attempt has been made to examine them for periodic trends of temperatures and salinities.

For the purpose of this discussion the inlet is divided into three regions, the head, the middle (mid-inlet), and the mouth.

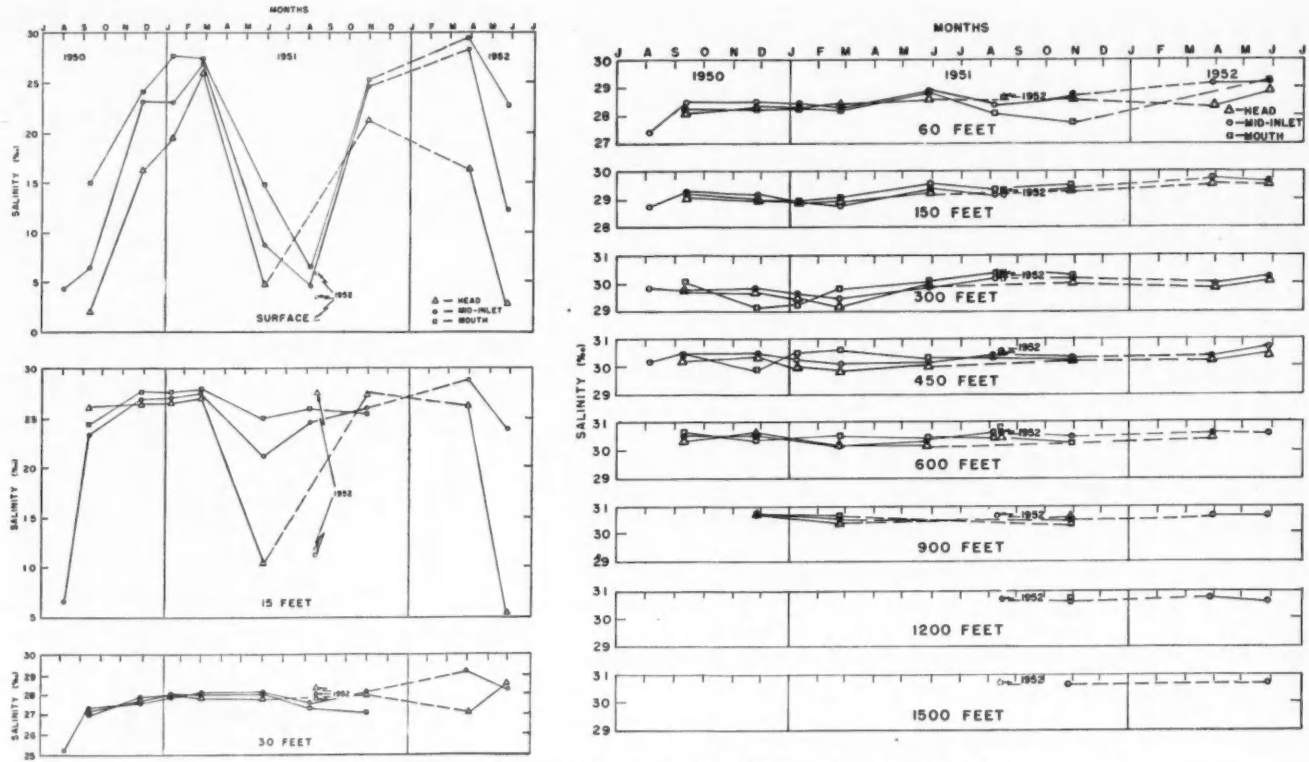


FIG. 18. Seasonal values of salinity at surface and below surface in Bute Inlet.

Variation of Salinity

In Fig. 18 are shown the seasonal values of the salinity of the surface and subsurface waters of Bute Inlet. The most pronounced feature is that the seasonal fluctuations, while very marked at the surface throughout the inlet, are conspicuous only to a depth of 15 feet at the head and at mid-inlet. They are less marked below the depth of 60 feet and almost negligible below 300 feet.

The water between the depths of 60 and 300 feet is about 0.6‰ more saline in the second year (August 1951 to May 1952) while the water between the depths of 450 and 900 feet had the same salinity.

The reason for these changes in salinity is that runoff and precipitation vary during the year. It is generally and tacitly assumed that river runoff only is indicative of fresh water supply, but precipitation on the water surface and on the immediate watershed may be significant. The only discharge data available for the Homathko River are for the years 1930–1932 (Anon., 1930–32) and then only for the outlet of Tatlayoko Lake (Fig. 19). Since there are many significant contributions to the river between Tatlayoko Lake and Bute Inlet it is probable that the actual discharge is many times that indicated. In fact the volume of fresh water which is transported into the inlet by the two rivers at the head was estimated by rough measurements of current and river cross-section to be as large as 14,000 cubic feet per second during the late spring in 1951, while recent estimates by Trites (1955) range as high as 20,000 cubic feet per second.

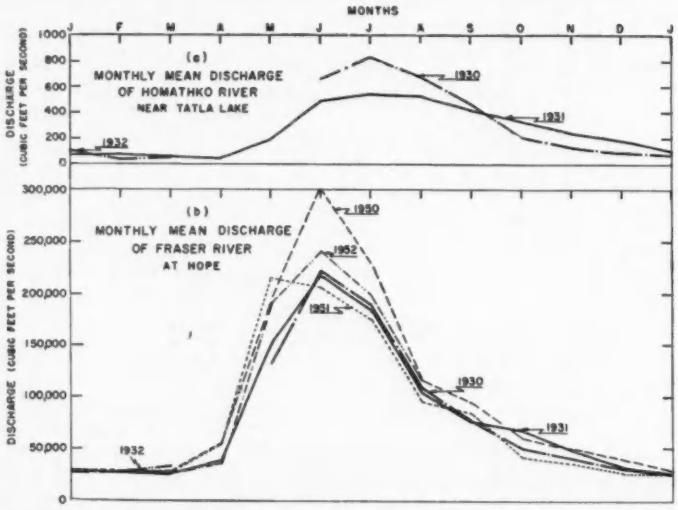


Fig. 19. Monthly mean discharges of (a) Homathko River near Tatlayoko Lake (1930–1932) and (b) Fraser River at Hope (1930–1932, 1950–1952).

On comparing the discharge of the Homathko River with that of the Fraser River, it is apparent that the curves of the monthly mean discharges plotted against time are similar in shape except that the peak discharge of the Homathko occurs

one month later than that of the Fraser. The discharge data for the Homathko have been estimated by assuming them to have the same ratio to those of the Fraser in 1950–1952 as they had in 1930–1932. Now, the drainage area into Bute Inlet is about 375 square nautical miles, not including that portion which is covered by the drainage area of the Homathko and Southgate Rivers. If all the water from precipitation within this area drains into the inlet the volume of fresh water entering the inlet will be appreciable (13,400 cubic feet per second for precipitation of one inch per day). However, as there are factors such as evaporation, land and vegetation storage, etc., it is difficult to estimate the percentage of precipitation that will actually drain into the inlet.

For the purpose of the present discussion, however, it is assumed that about 50% of the precipitation drains into the inlet, unless the land is saturated with moisture). Then the runoff D due to drainage may be expressed as $D = 6700\ r$ cubic feet per second where r is the rainfall in inches per day.

The direct precipitation falling into the inlet of area about 80 square nautical miles can be expressed as $P = 2800\ r$ cubic feet per second. The total amount of fresh water from drainage and precipitation will be $D + P = 9500\ r$ cubic feet per second.

The average rainfall per day (12-year means) at Waddington Harbour at the head of the inlet during the winter, spring, summer, and autumn is 0.24, 0.13, 0.07, and 0.26 inch, respectively (Climate of B.C., Department of Agriculture, 1955). This is equivalent to discharges of 2,300, 1,200, 670 and 2,500 cubic feet per second.

It is readily seen by comparing the incidental drainage plus precipitation during the spring and summer with the runoff from the Homathko and Southgate Rivers that their contribution is the predominant factor in the dilution of the inlet water. Hence during spring and summer and perhaps early autumn the precipitation and incidental drainage may be neglected. However, when river runoff is low, as it is during the winter, then precipitation should be considered. A large precipitation such as 2.72 inches in one day recorded at Thurlow Island during the late autumn of 1951 (Monthly Record, Meteorological Observations in Canada, 1951) which is equivalent to a runoff of 25,800 cubic feet per second, if applicable to the whole drainage area would almost certainly be the predominant factor in the dilution of the inlet waters at such a time.

Variation of Temperature

It is reasonable to compare air temperature with that of sea temperature regarding the former as a measure of heat input. For this purpose, the meteorological station at Thurlow was originally selected as a reference station to obtain air temperature because of its proximity to Bute Inlet, but since the observations at this station were discontinued in May 1951, Comox and Powell River have been selected. The monthly mean temperatures at these stations were obtained from the Monthly Record, Meteorological Observations in Canada, Department of Transport, Meteorological Division, Canada, and are shown in Fig. 20.

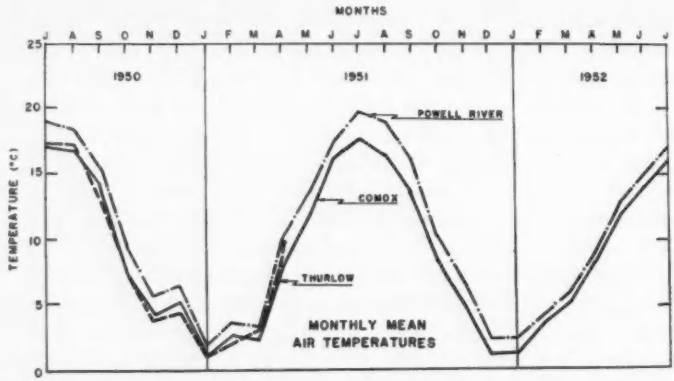


FIG. 20. Monthly mean air temperatures at Thurlow, Comox, and Powell River (1950–1952).

The temporal variations of the temperature at the surface and at depths to 1,800 feet are shown in Fig. 21. It is seen that there are marked seasonal variations which are in phase with those of the air temperature at the surface and to a depth of 150 feet and possibly to 300 feet, but below this the data are inadequate to determine if fluctuations are periodic or random.

On comparing the monthly mean air temperatures with the means of sea surface temperatures of this inlet, a good phase agreement is found which indicates that the sea surface temperature in Bute Inlet follows the climatological trend of this region, as has been shown to be the case for the waters of Georgia Strait (Pickard and McLeod, 1953).

These periodic variations are attributed mainly to the variations in the strength and the extent of insolation during the seasons. The water at and near the surface is generally cold at the head and gets warmer as it progresses toward the mouth, being warmed by insolation and also by mixing with the warmer water of the inlet.

As seen from Fig. 21, for the surface and the subsurface waters (to 15 feet) at the head, mid-inlet and the mouth the rates of warming and cooling are complementary during the spring and autumn respectively, the value being about 2 degrees per month.

The monthly mean surface water temperature at Yuculta Landing (September 1950–September 1951) are also plotted against time and are shown in Fig. 21. The water at Yuculta Landing is 2 to 3 degrees warmer than the surface water of Bute Inlet during the winter and is 3 to 4 degrees colder during the summer. This is no doubt due to the pronounced vertical mixing in the Yuculta Rapids.

It is apparent from these results that in Bute Inlet the determining factors causing the fluctuations in the temperature of the surface and subsurface waters are insolation and the cold inflowing fresh water.

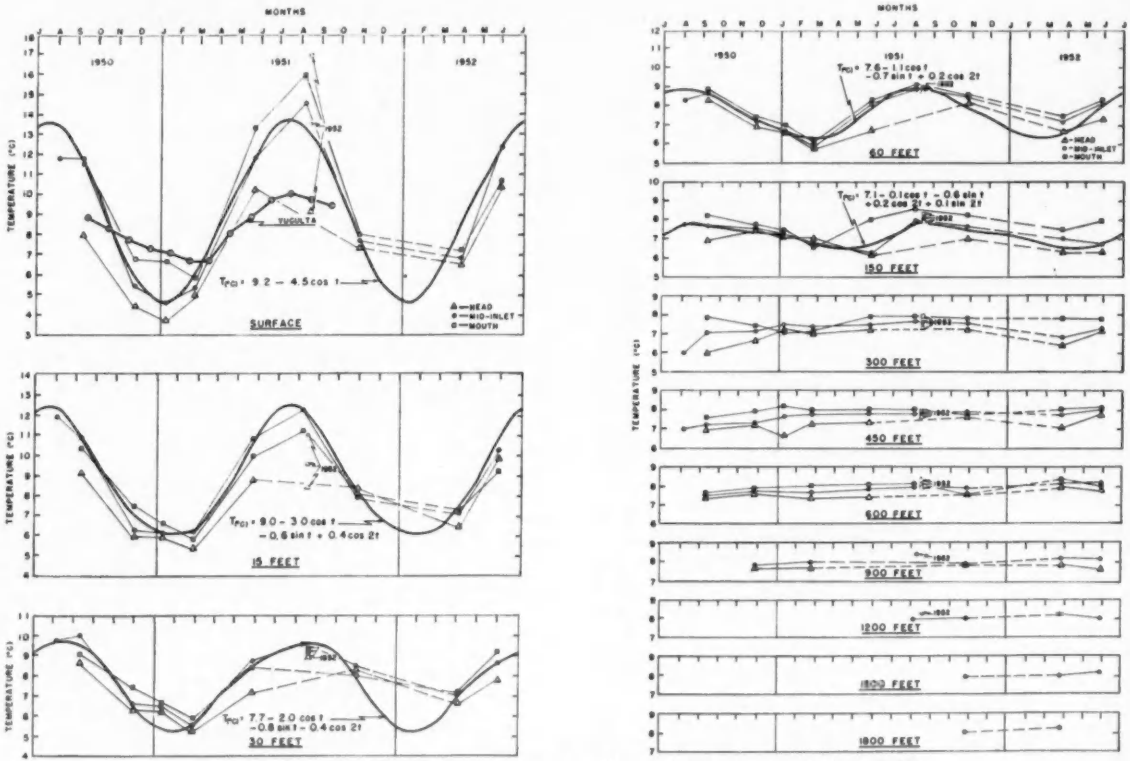


FIG. 21. Seasonal values of temperature at surface and below surface in Bute Inlet.

Analysis of the Long-Term Variation

Using the temperature data from mid-inlet, an equation may be fitted to the observed values to express the annual variations of the surface temperatures of this inlet.

The following equations are the results of this analysis for the changes occurring at mid-inlet at the indicated depths:

Depth (*feet*)	Temperature (° C.)
0	$T_0 = 9.2 - 4.5 \cos t,$
15	$T_{15} = 9.0 - 3.0 \cos t - 0.6 \sin t + 0.4 \cos 2t,$
30	$T_{30} = 7.7 - 2.0 \cos t - 0.8 \sin t - 0.4 \cos 2t,$
60	$T_{60} = 7.6 - 1.1 \cos t - 0.7 \sin t - 0.2 \cos 2t,$
150	$T_{150} = 7.1 - 0.1 \cos t - 0.6 \sin t + 0.2 \cos 2t + 0.1 \sin 2t$

where t represents the phase angle, taking January 10 as 0° and increasing by 30° monthly. These curves are drawn in Fig. 21.

VII. EDDY CONDUCTIVITY

References have been made previously to the minimum-temperature layer occurring at depths that vary from 125 to about 400 feet. This cold layer whose minimum temperature is about 6° C., appears as a tongue of cold water extending from the head almost to the mouth of the inlet, and gradually increasing in temperature seaward until it becomes indistinguishable near the mouth (Fig. 6b). The temperature of this layer generally increases with time from its inception in the Spring Transitional period (March) until it becomes indistinguishable in winter (January, February).

The minimum-temperature layer must be subject to heat influx from both the overlying and the underlying water. From the distribution of temperature adjacent to this layer an eddy coefficient of heat transfer (eddy conductivity) has been calculated.

At the depth near the minimum-temperature layer, the transverse temperature distribution is generally uniform and since the vertical temperature gradients are much larger than the horizontal temperature gradients, the heat transfer in the horizontal direction may be neglected. It is assumed that at the depth considered the horizontal advection terms may be neglected also.

Assuming A_z/ρ to be constant at the depth considered and vertical velocity to be negligible compared to the eddy transfer, the heat transfer equation reduces to

$$\frac{\partial T}{\partial t} = \frac{A_z}{\rho} \times \frac{\partial^2 T}{\partial z^2},$$

where T = sea temperature in ° C.,
t = time in months,
A_z = vertical eddy coefficient in g./cm./sec.,
ρ = density of sea water in g./cm.^{3}, and
z = vertical distance in metres.

For numerical computation this is approximated by a difference equation

$$A_z = \rho \frac{\Delta T}{\Delta t}\left(\frac{(\Delta z)^2}{T_1+T_2-2T_0}\right),$$

where $\Delta T/\Delta t$ = change of temperature in Centigrade degrees/month, and T_1 and T_2 are temperatures at equi-distant depths, Δz, (metres) above and below z_0 respectively. T_0 is the temperature at depth z_0 at which the second derivative is required, and ρ is taken as 1 g./cm.^{3}. The temperature T_0 is obtained from the temperature–depth curve at the depth where the temperature gradient $\Delta T/\Delta z$ is largest.

The values calculated for A_z are given in Table II (reduced to C.G.S. Units).

In the layer of water above the minimum-temperature layer where the stability ($E' = 10^5 \frac{d\sigma_t}{dz}$) is 2800/m., the average value of the coefficients is 0.65 g./cm./sec., while in the layer of water below the minimum-temperature layer and of lower stability 600/m., its value is 0.58 g./cm./sec. As shown in Table II, there are appreciable variations, although the order of magnitude remains the same.

TABLE II. Coefficients of vertical eddy conductivity (A_z) above and below the minimum-temperature layer.

Date	$\frac{\Delta T}{\Delta t}$	Above minimum temperature layer			Below minimum temperature layer		
		Depth	Stability $10^5\left(\frac{d\sigma_t}{dz}\right)$	A_z	Depth	Stability $10^5\left(\frac{d\sigma_t}{dz}\right)$	A_z
	degrees/month	*m.*	*m.*$^{-1}$	*g./cm./sec.*	*m.*	*m.*$^{-1}$	*g./cm./sec.*
Aug. 1950	0.42	30	4400	0.74	110	500	0.58
Sept. 1950	0.42	30	4000	1.47	110	300	1.25
May 1951	0.21	20	3400	0.74	90	700	0.23
Aug. 1951	0.26	40	1700	0.20	90	1000	0.63
Oct. 1951	0.26	80	1000	0.56	130	500	0.55
Aug. 1952	0.21	50	2200	0.17	110	400	0.21
Means	0.30	42	2800	0.65	107	600	0.58

For comparison, values of eddy conductivity calculated by Jacobsen (1913) for the vicinity of Schutz's Grund Lightship are shown in Table III. It may be seen that where the stabilities are comparable the coefficients of eddy conductivity for the water of Bute Inlet have values which are of the same order of magnitude as those given by Jacobsen.

TABLE III. Numerical values of eddy conductivity coefficient A_z as derived from observed time and space variations of salinity at Schutz's Grund (Jacobsen, 1913).

Depth	Horizontal currents	Stability ($10^5\ d\sigma_t/dz$)* at Station Da-21 (56°07.9′N., 11°11.1′E.)	Stability ($10^5\ d\sigma_t/dz$)* at "Schultz's Grund" lightship (56°08.9′N., 11°11.2′E.)	A_z
m.	*cm./sec.*	$m.^{-1}$	$m.^{-1}$	*g./cm./sec.*
0	7.8	...	...	...
2.5	6.4	12,000	8,000	0.3
7.5	1.7	12,000	20,000	0.18
12.5	7.6	110,000	100,000	0.04
17.5	13.3	72,000	50,000	0.74
20	17.4	...	...	...
23	...	...	8,000	2.1
25	...	8,000	...	...

*Computed from Jacobsen (1913), assuming temperature of water to be 5° C.

VIII. SUMMARY AND CONCLUSIONS

The salinity structures of the shallow water during the various seasons can be classified into two main groups, those occurring at periods of small runoff (winter) and those occurring at periods of large river runoff (summer).

As in other estuaries of this character the surface salinity generally increases with distance from the head to the mouth. During heavy runoff periods this increase in salinity is from 1‰ at the head to 15‰ at the mouth while during reduced runoff it is from 20‰ to 29‰. The surface salinity reaches a maximum during the winter, corresponding to the lowest river runoff, and attains a minimum during the summer when the runoff is largest. The surface water along the right-hand shore (looking seaward) is almost always observed to be less saline than that along the other shore. This is attributed to the effect of the Coriolis force. The progressive seaward increase in salinity in the upper layer is attributed to the gradual mixing of salt water with the surface waters of the inlet. During all seasons the salinity increases with depth. The most marked feature in the seasonal salinity variation is that while it is well marked at the surface, no regular cycle below 60 feet is evident. During periods both of small river runoff and large river runoff the salinity of the deep water is 30.6 to 30.8‰.

The temperature distributions for the different seasons may be grouped generally under the headings of winter and summer. The horizontal and vertical temperature distributions are less simple than those of salinity. In the shallower depths the temperature generally increases to seaward from the head to the mouth during all seasons. During the winter the temperature increases with depth from the sea surface to a maximum at mid-depths, then slowly decreases toward the bottom. However, during the summer it decreases rather rapidly at depths corresponding to the halocline, and then decreases more slowly to a well-defined minimum at intermediate depths. From this depth it increases to a maximum which is similar to that found during the winter, and then decreases slowly toward the bottom. The minimum-temperature pattern is less evident near the mouth.

The seasonal temperature variation of the surface and subsurface waters is in phase with the seasonal air temperature cycle and follows the climatological

trend of the locality. This variation is well marked in the surface layer and to a depth of 150 feet and possibly to a depth of 300 feet, but below this depth the water changes very little in temperature during the year. Insolation and the cold runoff water from the rivers are the predominant factors in determining the fluctuations in the temperature.

The concentration of dissolved oxygen is usually very high in the surface layer with maxima of 90% to 130% occurring near the mixing depth but not necessarily coinciding with it. The high oxygen values above 100% in the surface layer are associated with phytoplankton blooms. The waters at the greater depths are not stagnant as evidenced by the degree of oxygen saturation (40%).

There are three characteristic water masses in this inlet as follows:

(a) The Runoff Water which is the fresh water from river discharges,
(b) The surface Winter Water which is formed during the winter, and
(c) The Deep Water, which has a salinity over 30‰ and a temperature of about 8° C., and which changes little during the year.

Three distinct layers in the oceanographic structures in the water masses are evident. The upper layer of low salinity is formed by the mixing of saline water of the inlet with the fresh river water. Below this layer lies the mixed layer which is essentially the Runoff Water which has undergone more intensive mixing with the deeper water. The layer below this is broadly classed as the Deep Water lower layer, a body of high salinity water which does not change much in its structure compared to the other layers.

The shallow well-defined upper layer which is present during the runoff periods is absent in the winter owing to the reduction in runoff. However, in its place a well-mixed homogeneous layer of intermediate salinity is formed.

During the year only one main circulation pattern is presumed. This is the general estuarine circulation in which there is a net down-inlet flow in the upper layer accompanied by a net up-inlet flow below this layer. This flow occurs throughout the seasons although it is less pronounced during the winter.

Eddy coefficients of conductivity have been computed using a simplified conduction formula. The values determined vary from 0.2 to 1.5 g./cm./sec., for the intermediate depths. These values are of the same order as those determined, for instance, by Jacobsen for Danish waters of similar stability.

ACKNOWLEDGMENTS

The authors wish to express their acknowledgments to the Fisheries Research Board of Canada for financial assistance, to the National Research Council for grants-in-aid, and to the Royal Canadian Navy for providing ships. They are grateful for the help and co-operation received from the officers and men of H.M.C.S. *Cedarwood* and C.N.A.V. *Ehkoli* during the field work, and particularly wish to thank Dr. J. P. Tully, Oceanographer in Charge, Fisheries Research Board, Pacific Oceanographic Group, for making cruise data available and for his advice and helpful criticism. They are also indebted to Miss Beverley Berisford for preparing the typescript.

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The Qualitative and Quantitative Distribution of Plankton in the Strait of Georgia in Relation to Certain Oceanographic Factors[1,2]

By Joseph Eugène Henri Légaré

The University of British Columbia, Vancouver, B.C.

ABSTRACT

In order to gain some picture of the seasonal variations in the plankton communities two cruises were made in the Strait of Georgia, one in June 1955, and the other in November 1955; 165 plankton collections were taken, also surface temperatures.

The correlation of these data have resulted in a number of conclusions concerning the distribution of plankton in the Strait of Georgia. The chief factor affecting the general distribution of plankton is the salinity gradient. The inflow of fresh water from the Fraser River forms zones of varying properties, and leads to the development of different plankton communities. The extent to which physical and chemical factors may determine the presence or absence of certain organisms from the zones described is discussed.

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INTRODUCTION

The Strait of Georgia (Fig. 1) occupies a position of considerable interest for the study of plankton because, within its limits it presents an unusual complexity of conditions which differ greatly from summer to winter. In summer the fresh water from the Fraser River flows into the Strait and spreads over the surface in cloud-like distribution, mixing with the saline water to form a brackish upper layer which is well differentiated from the more saline, homogeneous waters underneath. In winter the river discharge diminishes and most of the water in the Strait reaches an homogeneous state.

[1]Received for publication July 5, 1956.

[2]Based on a thesis submitted to the University of British Columbia in partial fulfilment of the requirements for the degree of Master of Arts.

[3]Author's present address: c/o Station Zoologique, Villefranche-sur-Mer (Alpes-Maritimes), France.

J. Fish. Res. Bd. Canada, 14(4), pp. 521–552, 1957.
Printed in Canada.

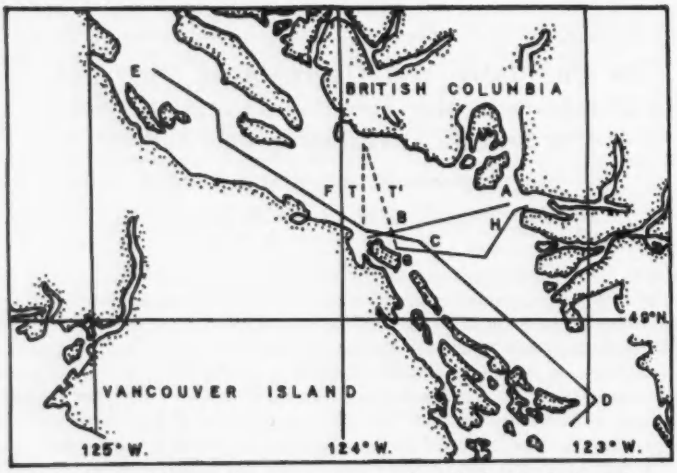

FIG. 1. Strait of Georgia showing sections made with the Hardy Recorder.

In accordance with the complexity of conditions, the distribution of species is intricate and their relative abundance fluctuates widely from place to place and from time to time. Cameron and Mounce (1922) found that some species exhibit a difference in morphological character and rate of growth which can be traced to different physical and chemical conditions, and showed that the Fraser River was responsible for most of the conditions peculiar to these waters. Lucas and Hutchinson (1927) came to the conclusion that diatom optima exist where the Fraser River water and the sea water are mixed. It has already been pointed out by Hutchinson (1928) that the richness of the plankton flora is largely dependent on the Fraser as a source of silica and also upon the conditions which conserve this material. Tully and Dodimead (1957) also discuss diatom distribution in terms of dissolved oxygen, pH and dissolved nutrients. They attribute the high concentrations of dissolved phosphates to the intruding ocean waters, and the high concentrations of dissolved silicates to the Fraser River waters. This paper evaluates qualitatively and quantitatively the organisms responsible for the abundance of both phytoplankton and zooplankton and assesses the physical and chemical factors affecting their distribution.

ACKNOWLEDGMENTS

The writer wishes to express his sincere thanks to the following: The National Research Council for providing financial assistance during the period of this study; to Dr. R. F. Scagel for his help throughout the entire progress of the work; Dr. M. Waldichuk, for the use of extensive unpublished data on the physical oceanography of the Strait of Georgia; and the Master and crew of the C.N.A.V. *Ehkoli* for their assistance and co-operation.

DISTRIBUTION OF PHYSICAL AND CHEMICAL PROPERTIES OF THE WATERS IN THE STRAIT OF GEORGIA

Salinity

The range of salinities existing in the surface waters of the Strait of Georgia varies from 1‰ at the Fraser River estuary to 25‰ at the northern and southern extremities (Waldichuk, 1955). The fresh water flowing into the Strait from the River spreads over the surface, mixes with the saline water, and forms an upper, brackish silty layer referred to as the "upper zone" (Tully and Dodimead, 1957). Below the upper zone there is a layer of fairly homogeneous salinity, referred to as the "lower zone", and between the upper zone and the lower zone, there is a transition layer, referred to as the "boundary zone". This boundary zone is characterized by a steep gradient of salinities.

Temperature

Surface temperatures in the Strait of Georgia for June, 1955, are given in Fig. 2. The southern Strait exhibits the lowest temperature (12.4° C.). The surface water is cold near the Fraser River estuary (12.8° C. at Station 12). The highest temperature (15.8° C.) is recorded off Gabriola Island.

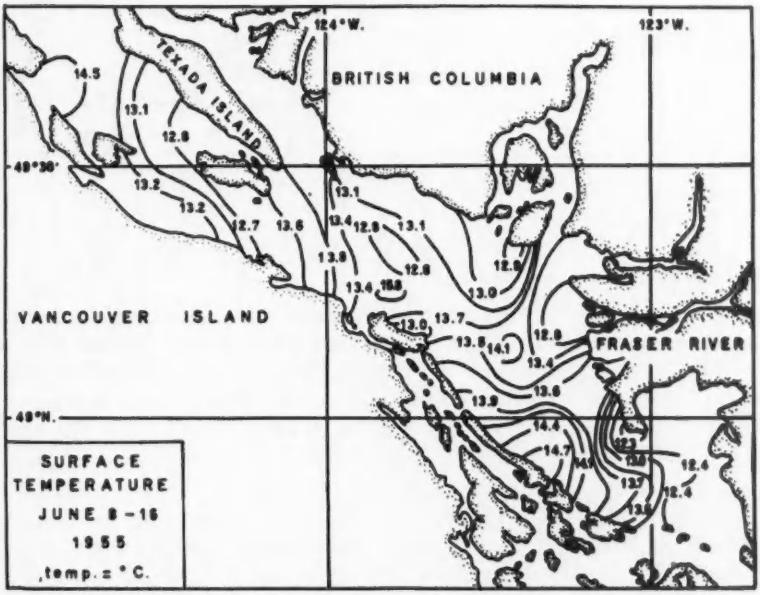

Fig. 2. Surface temperatures, June 8–16, 1955.

Generally, surface temperatures are lower in the eastern portion of the Strait along the mainland and higher in the western portion of the Strait. The surface gradient over the whole area was only 3.4° C. in June 1955. Surface temperatures

in November (Fig. 3) are fairly uniform over the central part of the Strait. The northern waters are a little warmer, with a difference of temperature over the Strait of only 0.9° C. (ranging from 8.5° C. to 9.4° C.).

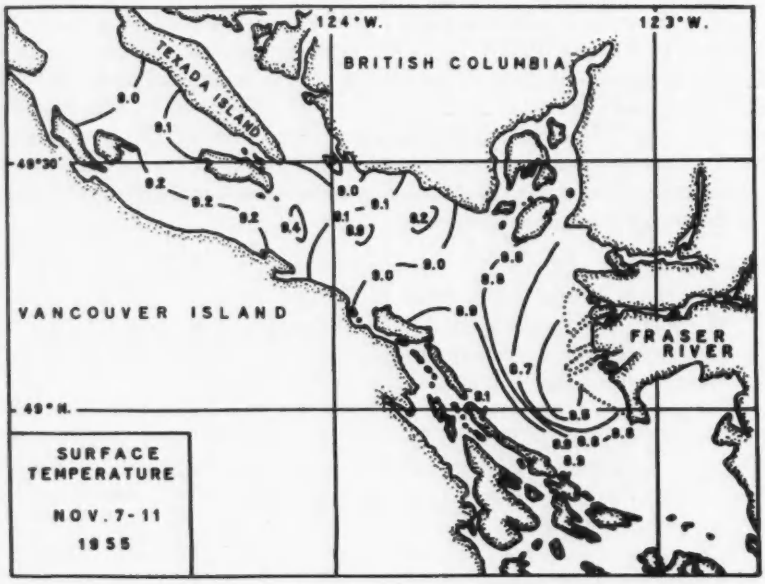

FIG. 3. Surface temperatures, November 7–11, 1955.

MATERIALS AND METHODS

AREA COVERED

The data presented are based on 165 plankton collections taken in the Strait of Georgia during two cruises—one in early summer, from June 8 to 16, 1955, and one in the fall, from November 7 to 11, 1955. The first cruise covered 38 stations distributed throughout the Strait from the San Juan Islands to the northern end of Texada Island. However, as a result of bad weather conditions at the time of the fall cruise, it was possible to reoccupy only 26 of the 38 stations established on the earlier cruise. The stations occupied are distributed between 48° 48′ and 49° 40′ N. Lat. and between 122° 50′ and 124° 45′ W. Long. (Fig. 4, 5).

At all but three stations two vertical hauls, using a plankton net (Fig. 6), were made. The first haul was always taken in one of three shallower depths (from 10, 20, or 50 metres to the surface) to prevent contaminating the net with deeper plankton species, and a deeper haul was taken through strata varying from 50 to 250 metres to the surface. Surface temperatures were obtained at all stations at which plankton samples were taken. Compass bearings were taken at the start of each haul. Records of sonic depth, wind velocity, barometer readings

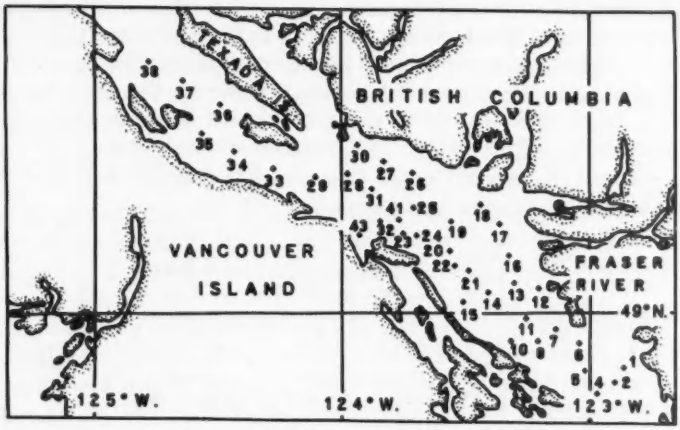

FIG. 4. Location of Stations, June 8–16, 1955.

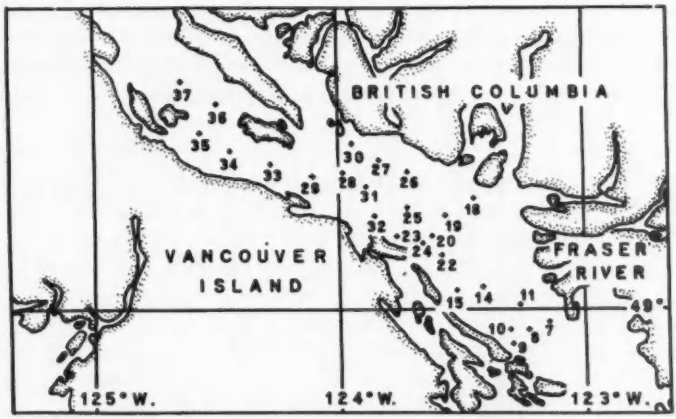

FIG. 5. Location of Stations, November 7–11, 1955.

and cloud coverage were kept. A few stations were omitted during the two cruises in order to give maximum coverage of the Strait.

In addition to the vertical hauls, horizontal sampling was carried out with the Hardy Recorder during the first cruise. The object in using the Hardy Recorder was to determine the horizontal changes in the major constituents of the plankton over the areas investigated between the stations at which the vertical hauls were made.

SAMPLING METHODS

To determine the vertical limits of distribution of the main constituents a plankton net was used (Fig. 6). The net measures 20 inches in diameter at the

mouth, 60 inches in length, and 4 inches in diameter at the cod-end. A jar having a volume of 500 cc. is held tightly at the small opening by a metal clip. A string (6a) joins the metal clip to a 50-pound lead weight to keep the net from turning inside out when lowering. The weight is suspended from the lower end of three ropes (6b). These ropes, which pass alongside the net, are tied around the metal ring forming the mouth of the net, and are attached above the mouth of the net to the oceanographic cable. The net is made of bolting silk No. 25 XXX. The same net was used throughout both cruises.

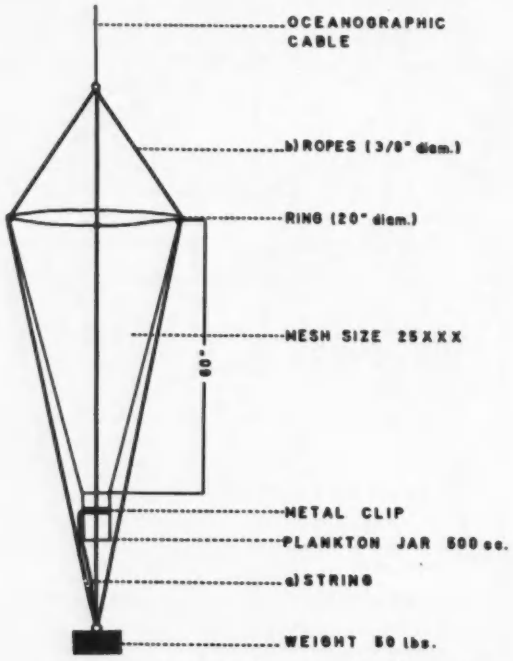

FIG. 6. Diagram of plankton net used in the survey.

VERTICAL HAULS

The shipboard procedure followed upon reaching a station involved first reversing the engine to bring the vessel to a complete stop. Some leeward motion of the ship was encountered while the sampling was being carried on, but this minor drift was disregarded.

All sampling was performed from the starboard side of the after deck. The ship was provided with a powered winch and a metre block.

The net was lowered slowly at a uniform speed and, upon reaching the desired depth it was also retrieved at a slow, uniform speed. When the net reached the surface it was lifted out of the water and while still suspended from

the oceanographic boom it was washed down with three or four buckets of sea water. The plankton jar was then detached and the sample was transferred to a glass jar. The organisms clogging the net were washed free with a wash-bottle. Some formalin at 5% concentration was then added to the sample and a label was placed in the jar.

HARDY RECORDER TOWS

The instrument consists of two elements, the external torpedo-shape body weighing several hundred pounds and the internal removable mechanism. The body is fitted with two ailerons and one elevator, so that when it is towed it will dive and maintain itself at uniform depth (Hardy, 1939).

When launching the Recorder the ship was stopped and the instrument was slowly lifted over the rail. This was done by using the main boom of the ship to lift the instrument and at the same time swing it clear of the stern while it was being lowered. When the Recorder touched the water the block and tackle was detached, and the towing cable played out to a mark placed on it at a point calculated to give a sampling depth of ten feet. The towing speed used varied from 8 to 9 knots. At launching and at hauling the position and time were recorded. When the haul was completed the Recorder was hoisted inboard and the used section of silk was removed. The silk was then transferred to a glass jar and formalin at 5% concentration was added.

Laboratory Methods

All the zooplankton samples were analysed in the laboratory with a binocular microscope using a 40× magnification, and all the phytoplankton species were identified with a compound microscope using 100× magnification. The following treatment was used in analysing the samples:

1. The plankton sample was well shaken and 5 cc. were removed with a pipette having a length of 30 cm. and a diameter of 8 mm. A complete count of the zooplankton in the 5 cc. sample was made and tabulated as follows: all copepods to species and sex; nauplii, metanauplii, calyptopis, furcilia, cyrtopia, and adult stages of euphausids; all other major taxonomic groups including appendicularians, chaetognaths, amphipods, gastropods, ostracods, cladocerans, eggs, and larvae.

2. The qualitative analysis of the phytoplankton was made by placing a few drops of the original sample in a ruled chamber and scanning the whole field. After the entire chamber had been examined a new sample was drawn and from this chamber, which has a volume of 166 cubic millimetres, counts were made for each species. When the quantities of phytoplankton cells were great, one-sixth of the volume was counted, when they were small the number of cells in 166 cubic millimetres was counted.

3. In addition to the normal procedure outlined in 1 and 2 above, a total count was made of all adult euphausids, chaetognaths and amphipods in each sample taken on the November cruise.

4. The silk taken from the Hardy Recorder was cut into sections each of which represents a horizontal haul over a distance of three to five miles. The plankton was then removed from each section. The large organisms were removed by hand, the smaller ones with a razor blade, and transferred to 100 cc. of water. A total count of all the zooplankton was made from each section of silk. The phytoplankton was analysed and counted as outlined in 2 above.

COMPOSITION OF THE PLANKTON

Zooplankton Taken in the Summer Cruise, June 8–16, 1955.

Some 34 species of copepods, of three sub-orders, were taken:

Sub-order CALANOIDA

Acartia clausi Giesbrecht, *A. longiremis* (Lilljeborg), *Celanus cristatus* (Krøyer), *C. finmarchicus* (Gunnerus), *C. tonsus* Brady, *Candacia columbiae* Campbell, *Centrogaptilus porcellus* Johnson, *Centropages mcmurrichi* Willey, *Chiridius tenuispinus* Sars, *Diaptomus* sp. Westwood, *Epilabidocera amphitrites* (McMurrich), *Eucalanus bungii* Giesbrecht, *Euchaeta japonica* Marukawa, *Eurytemora hirundoides* (Nordquist), *E. johanseni* Willey, *Gaidius pungens* Giesbrecht, *Metridia longa* (Lubbock), *M. lucens* Boeck, *Microcalanus pusillus* Sars, *Paracalanus parvus* (Claus), *Pseudocalanus minutus* (Krøyer), *Scolecithricella minor* (Brady), *Tortanus discaudatus* (Thomson and Scott).

Sub-order CYCLOPOIDA

Ascomyzon rubrum Campbell, *Corycaeus affinis* McMurrich, *Oithona helgolandica* Claus, *O. plumifera* Baird, *Oncaea conifera* Giesbrecht.

Sub-order HARPACTICOIDA

Diosaccus spinaeus Campbell, *Harpacticus uniremis* Krøyer, *Idya furcata* (Baird), *Microsetella rosea* (Dana).

A few rare species of a number of genera were met in the samples, which were not identified because of taxonomic difficulties.

Several phyla were represented by many genera but no attempt was made to determine these beyond major groups. The following 26 groups were analysed in this way:

Amphipods, Annelids, Appendicularians, Barnacle larvae, Chaetognaths, Cladocerans, Copepod larvae, Crab larvae, Clam larvae, Eggs, Euphausid larvae, Fish larvae, Gastropods, Holothurians, Hydromedusae, *Mysis*, Ostracods, Planula of coelenterates, Pluteus of brittle stars, Polychaete larvae, Pteropod larvae, Shrimp larvae, Siphonophores, Snails, Tintinnidae–observed but not analysed, Unidentified triangular egg case.

Protozoans were also found in a few samples. The mesh size of the net was too coarse to retain these organisms in any quantity and no attempt was made to study their distribution. A few radiolarians were observed, among them were:

Ceratium furca (Ehrenberg), *Dinophysis hastata* Stein, *Distephanus speculum* var. *regularia* Lemmerman, *Gonyaulax spinifera* (Claparède and Lachmann), *Nematodinium armatum* Dogiel.

Percentages, by numbers, of seven constituents of the zooplankton are given in Table I. In almost all samples copepods were the most abundant of all constituents. The appendicularians (*Oikopleura* spp.) were second in abundance, followed by euphasids, eggs, chaetognaths, gastropods and amphipods. Next, but

not included in this table, were the larval stages of barnacle, crab, ostracods, cladocerans, hydromedusae, annelids, polychaete larvae, fish larvae and other, less frequent forms. At a few stations there occurred large numbers of other specific groups, such as siphonophores and *Littorina*, but in each case these were local populations and did not contribute to any extent to the overall distribution.

PHYTOPLANKTON TAKEN IN THE SUMMER CRUISE, JUNE 8–16, 1955.

Forty-five species of diatoms were found. The following list is not complete and in a few cases the identification to species is somewhat uncertain. Some slight differences of opinion on the taxonomy of certain species are found in the literature (Fran and Angst, 1931; Cupp, 1943) which render the identification of

TABLE I. Percentages, by numbers, of seven constituents of the zooplankton, June 8–16, 1955.

Stn. No.	Depth	Eggs	Copepods	*Oikopleura*	Gastropods	Amphipods	Chaetognaths	Euphausids
	m.	%	%	%	%	%	%	%
1	10	12	45	36	1	1	—	1
1	50	15	68	12	—	1	—	1
2	10	7	30	46	—	1	1	4
2	80	20	48	20	3	—	—	3
4	10	10	20	58	—	—	1	2
4	100	10	61	17	4	—	—	3
5	20	3	50	23	—	—	2	2
5	200	4	82	5	4	—	—	1
6	50	5	29	32	1	—	—	7
7	10	30	33	12	1	1	1	3
7	90	25	69	2	1	—	—	—
8	50	6	67	4	4	—	—	12
8	110	3	76	7	4	—	—	5
10	10	27	11	55	—	—	—	—
10	150	11	51	26	3	—	—	2
11	10	—	69	12	—	—	—	14
11	100	4	65	14	1	1	—	9
12	10	—	64	10	—	—	—	10
12	50	12	60	15	—	—	1	2
13	10	—	88	7	—	—	—	—
13	50	6	72	8	—	2	—	3
14	20	5	22	64	—	—	1	2
14	200	3	63	24	3	1	—	2
15	10	5	27	58	1	—	2	1
15	150	3	58	24	6	1	—	2
16	10	—	87	4	—	1	—	7
16	100	—	80	4	3	1	—	9
17	20	5	79	6	—	1	3	3
17	150	4	78	7	4	1	—	4
18	10	—	59	8	1	1	1	22
18	150	5	73	2	12	—	—	3
19	50	3	69	10	—	1	5	1
19	200	4	77	2	2	2	—	6
20	20	17	54	15	—	—	—	4
20	250	8	71	5	2	2	—	4
21	20	6	64	9	—	2	—	11
21	150	3	66	8	—	1	—	13
22	10	17	31	37	—	—	—	6
22	100	2	55	23	5	—	1	2
23	10	49	37	3	1	—	1	—
23	100	17	74	2	2	—	—	—
24	20	23	54	13	—	—	—	2
24	50	18	62	9	1	1	1	3
25	10	35	49	8	—	—	1	2
25	20	17	69	5	—	—	1	2

TABLE I. – continued.

Stn. No.	Depth	Eggs	Copepods	*Oikopleura*	Gastropods	Amphipods	Chaetognaths	Euphausids
	m.	%	%	%	%	%	%	%
25	50	13	67	4	3	—	1	5
25	100	13	66	5	2	—	1	6
25	150	9	65	3	2	—	1	12
26	20	7	73	5	1	1	3	2
26	150	8	80	1	2	2	1	3
27	20	1	88	1	—	3	1	1
27	50	2	82	12	—	—	1	1
28	20	1	60	4	1	—	1	27
28	230	—	82	1	3	—	1	4
29	50	7	68	1	8	1	4	3
29	150	4	78	—	5	1	1	2
30	10	3	44	3	—	11	11	17
30	150	9	74	3	1	4	1	5
31	10	2	65	11	—	—	3	8
31	100	2	68	6	3	—	2	13
32	20	9	61	11	5	—	1	2
32	100	3	77	5	6	—	—	2
33	10	9	49	27	1	1	1	8
33	200	4	62	2	3	—	—	20
34	50	—	82	5	4	—	—	5
34	150	—	81	2	5	—	—	6
35	20	1	94	2	—	—	—	—
35	100	1	82	3	4	—	—	6
36	10	10	55	5	2	3	1	12
36	100	2	58	2	9	—	—	27
37	50	7	71	5	5	—	—	10
37	100	4	74	4	5	—	—	9
38	20	5	73	8	9	—	—	2
38	100	3	71	7	12	—	—	2
41	10	16	23	33	1	1	1	3
41	200	8	56	7	5	3	1	5
43	50	38	26	24	—	—	—	2

certain species, such as in the genus *Chaetoceros*, difficult. Nevertheless, it is possible to compare the relative abundance of most species in the area with the data available.

The following diatoms were identified:

Asterionella japonica Cleve, *Bacteriastrum delicatulum* Cleve, *Biddulphia aurita* (Lyngbye) Brébisson and Godey, *B. laevis* Ehrenberg, *B. longicruris* Greville, *Chaetoceros affinis* Lauder, *C. brevis* Schütt, *C. concavicornis* Mangin, *C. constrictus* Gran, *C. convolutus* Castracane, *C. curvisetus* Cleve, *C. debilis* Cleve, *C. decipiens* Cleve, *C. didymus* Ehrenberg, *C. lacinosus* Schütt, *C. lorenzanus* Grunow, *C. radicans* Schütt, *C. similis* Cleve, *C. teres* Cleve, *C. vanheurcki* Gran, *Corethron hystrix* Hensen, *Coscinodiscus excentricus* Ehrenberg, *C. wailesii* Gran and Angst, *Ditylum brightwellii* (West) Grunow, *Eucampia zoodiacus* Ehrenberg, *Fragilaria crotonensis* Kitton, *F. striatula* Lyngbye, *Grammatophora marina* (Lyngbye) Kützing, *Leptocylindrus danicus* Cleve, *Melosira monoliformis* (Müller) Agardh, *M. sulcata* Kützing, *Navicula* sp. Bory, *Nitzschia* spp. Hassal, *Pleurosigma* spp. Smith, *Rhizosolenia delicatula* Cleve, *R. hebetata* forma *semispina* (Hensen) Gran, *R. stolterfothii* Pérégallo, *R. styliformis* Brightwell, *Skeletonema costatum* (Greville) Cleve, *Stephanopyxis nipponica* Gran and Yendo, *Thalassionema nitzschioides* Grunow, *Thalassiosira condensata* Cleve, *T. decipiens* (Grunow) Jørgenson, *T. nordenskioldii* Cleve, *Thalassiothrix frauenfeldii* Grunow.

The dominant filamentous diatom genera found in June were *Skeletonema*, *Chaetoceros*, *Thalassiosira*, *Biddulphia*, and *Nitzschia*. The length of the filaments

could not be approximated. The formalin solution used made the filaments very brittle and most of them broke apart when the samples were shaken.

ZOOPLANKTON AND PHYTOPLANKTON TAKEN IN THE FALL CRUISE, NOVEMBER 7–11, 1955.

Some 35 species of copepods were present in varying abundance in the samples taken in the summer, whereas only 21 species were present in November, and in very much smaller quantities in the latter instance. Some species, such as *Calanus tonsus*, *Eucalanus bungii*, and *Centropages mcmurrichi*, which were very abundant in June, could not be found in the samples in November, although the same depths were sampled. Deeper forms, such as *Centrogaptilus porcellus*, *Harpacticus uniremis*, and *Idya furcata*, could not be found in November, even though the water, at such depths, is relatively uniform in physical and chemical characteristics throughout the year. One species, *Aetideus armatus*, was found in the fall, but was not observed in June.

Twenty-one species of copepods, of two sub-orders, were taken:

Sub-order CALANOIDA

Acartia clausi Giesbrecht, *A. longiremis* (Lilljeborg), *Aetideus armatus* (Boeck), *Calanus finmarchicus* (Gunnerus), *Candacia columbiae* Campbell, *Chiridius tenuispinus* Sars, *Epilabidocera amphitrites* (McMurrich), *Euchaeta japonica* Marukawa, *Eurytemora hirundoides* (Nordquist), *Gaidius pungens* Giesbrecht, *Metridia longa* (Lubbock), *M. lucens* Boeck, *Microcalanus pusillus* Sars, *Paracalanus parvus* (Claus), *Pseudocalanus minutus* (Krøyer), *Scolecithricella minor* (Brady), *Tortanus discaudatus* (Thompson and Scott).

Sub-order CYCLOPOIDA

Ascomyzon rubrum Campbell, *Corycaeus affinis* McMurrich, *Oithona* spp. Baird, *Oncaea conifera* Giesbrecht.

The percentage of adult and immature individuals was found to remain quite constant in June and in November. Fifty-three per cent of the summer catch was made up of adult specimens, as compared with 52% in the autumn. Many of the species found in autumn, such as *Calanus finmarchicus*, were therefore actively reproducing and not just surviving. The same is true for several other groups: immature specimens of amphipods, cladocerans, barnacles, and ostracods were found in the samples taken in November.

In addition to copepods, the main constituents of the zooplankton in November were:

Appendicularians, Cephalopods (egg cases), Chaetognaths, Cladocerans, Barnacle larvae, Clam larvae, Eggs, Euphausids, Gastropods, Holothurians, Hydromedusae, Nauplii, Ostracods, Polychaete larvae, Siphonophore larvae, *Tomopteris* spp., Unidentified triangular egg case.

Catches of chaetognaths and euphausids were made up entirely of adult specimens in November. The unidentified egg case was the next most abundant constituent of the zooplankton after the copepods. Next came the euphausids, chaetognaths, amphipods, gastropods, *Oikopleura*, ostracods, and hydromedusae. The other representatives were never abundant.

Only two species of diatoms obtained in November samples were significant. *Coscinodiscus wailesii* and *Chaetoceros concavicornis* were found in relatively

large numbers. There was a dearth of all other species. A few cells of *Chaetoceros affinis*, *Rhizosolenia semispina*, and *Nitzschia* sp. were also encountered. Out of 52 samples, only 13 gave values of more than 1 cell per litre and the maximum frequency never exceeded 10 cells per litre. No protozoans were seen in the plankton samples taken in November.

ABUNDANCE OF PLANKTON IN THE STRAIT OF GEORGIA

Zooplankton in the Summer Cruise, June 8–16, 1955.

To provide a basis for comparison of the total catch at any one locality, all quantities obtained from the 5 cc. samples quantitatively analysed were transformed into values based on a standard volume of one cubic metre. This was done by dividing the number of zooplankton per sample by the volume of water filtered. Since no device was used to record the amount of water filtered, it is assumed that the net was fishing vertically and no spilling occurred. With this assumption the number of cubic metres of water strained at each depth was then calculated. This method of calculation cannot give a complete evaluation of the zooplankton distribution with depth, but it points out with a reasonable degree of accuracy the areas of high, average, and low concentrations. The absolute concentrations computed in this way are too small, to a variable degree, since the fine-meshed net offered considerable resistance to passage of water, resistance which would vary with the abundance of plankton and amount of clogging of the meshes.

Based on the semi-quantitative evaluation of the zooplankton obtained in the above manner, three centres of different concentrations (Fig. 7) can be recognized and associated with the physical and chemical characteristics of the waters in the Strait of Georgia.

A. An area of high concentration at Stations 10, 11, 12, 13, 15, 21, and 22, with warm surface temperature (ranging from 13.5° to 14.7° C.) and strong mixing of water masses.

B. An area of intermediate concentration at Stations 16, 17, 19, 20, 23, 24, 25, and 32, with colder surface temperatures (from 12.8° to 13.7° C.) and little mixing of water masses.

C. An area of low concentration at Stations 18, 26, 27, 28, 29, 30, and 31, with still colder surface temperatures (from 12.4° to 13.6° C.) and little mixing of water masses.

The catches made in the tows between 50 metres and the surface were more characteristic of the Strait of Georgia because they included populations inhabiting both the "upper zone" and the uppermost stratum of the homogeneous "lower zone".

The catches proved to be fairly uniform from station to station, as far as the predominant species were concerned, and thus copepods were, in most cases, the most abundant animals. However, regional differences in the relative abundance of copepods, euphausids, amphipods and chaetognaths resulted in notable differences in the plankton population from station to station.

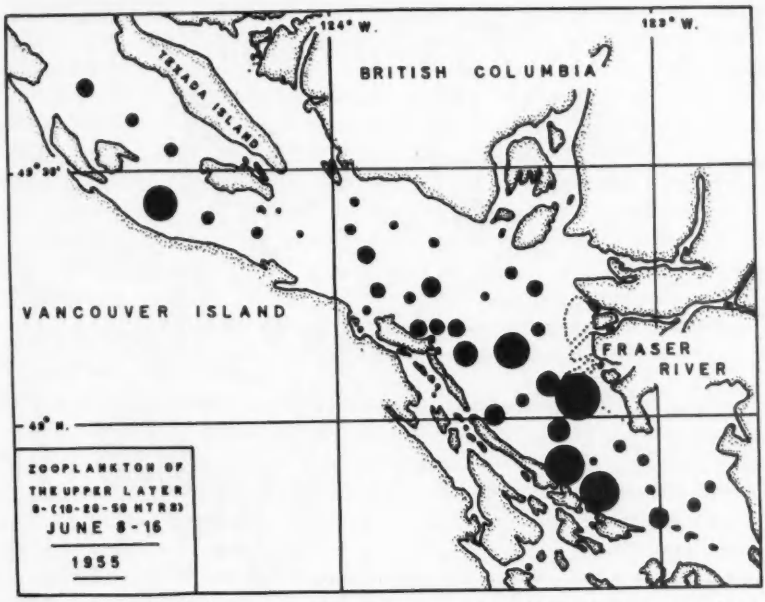

FIG. 7. Zooplankton abundance from surface to depths of 10, 20, and 50 metres, June 8–16, 1955.

In some instances, one or another species dominated. Thus, at Station 18, the copepod *Calanus tonsus* formed the bulk of the catch in the haul from 150 metres to the surface. Surface hauls at Stations 12, 13, 17, 35, 37, 38, yielded very large numbers of *Pseudocalanus minutus*. *Oikopleura* sp. was predominant at the surface at four stations (4, 6, 10, and 14) as were eggs at Station 10 in a haul from 10–0 metres.

PHYTOPLANKTON IN THE SUMMER CRUISE, JUNE 8–16, 1955.

It is impossible to state on the basis of a survey lasting only two weeks whether the conditions encountered in June 1955, are typical for this period of the year. The late spring and relatively cold June of 1955 may have affected the abundance of diatoms and delayed the period of peak abundance; according to van't Hoff's Law a 10° C. rise in temperature increases the rate of metabolism 2 to 3 times. Campbell (1929) found that temperature and plankton occurrence are definitely correlated within the limits of 10–15° C. Within these limits, at least, an increase in temperature is accompanied by an increase in plankton in the Strait of Georgia.

Although absolute abundance of diatoms during the period of this study is only a measure of the standing crop, it is probably indicative of a fairly productive area (Fig. 8). The maximum computed number of diatom cells per litre (124,480) in the Strait of Georgia does not compare with 20,000,000 cells re-

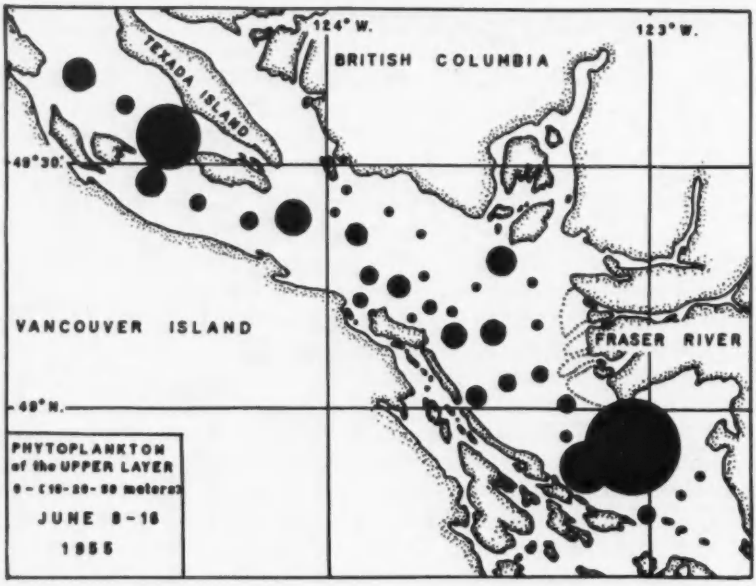

FIG. 8. Phytoplankton abundance from surface to depths of 10, 20, and 50 metres, June 8–16, 1955.

corded in the Clyde Sea in April 1927 (Marshall and Orr, 1927). The maximum computed volume of diatoms, obtained in June 1955, was 25 units per 100,000 units of water. The maximum volume reported by Hutchinson and Lucas (1931), on July 30, 1927, was 110/100,000. Hutchinson and Lucas used a pump to obtain their samples, and so had an accurate measure of the volume strained. Our net, when diatoms were abundant, might not have strained more than a quarter of the water column through which it was hauled, so that our biggest collections may be from populations as dense as those sampled by Hutchinson and Lucas.

Few diatoms were taken at Stations 13, 16, and 17 close to the Fraser River estuary (Fig. 8). This region is characterized by a low salinity and a high turbidity. The latter greatly reduces the depth of the photic zone which in turn affects the growth of phytoplankton. In the centre of the Strait the standing crop in June 1955, was higher in the western portion than in the eastern portion; only Station 18, located at the mouth of Vancouver Harbour, where more extensive mixing is taking place, showed a relatively high standing crop. Several authors (Hutchinson and Lucas, 1931; Tully, 1932; Waldichuk, 1952) have observed a larger flow of Fraser water along the eastern portion of the Strait bringing lower salinities to the area. Temperatures are also colder in this region (Fig. 2). The salinity gradient is therefore one of the chief factors affecting the general abundance of phytoplankton in this central region of the Strait.

The standing crop of the surface waters at Stations 35, 36, and 38 in the northern area was high. Tully (1932) found a decrease of phosphate concentration during the summer and low silicate values (1 mg./l. in July) in this area. This decrease in the chemical constituents can be attributed to phytoplankton activity and since the latter region is located in the less turbulent part of the Strait (Tully, 1954) it is evident that depletion of silicates will limit phytoplankton growth. Tully (1932) suggests that other nutrients do not reach concentrations low enough to limit the development of phytoplankton.

The highest standing crop appeared south of Point Roberts at Station 6. Hutchinson and Lucas (1932), and Waldichuk (1952), found that strong physical and chemical gradients existed in this region where fresh and salt water mixing occurs. Both fresh water and sea water masses contributed certain favourable factors for the rapid growth of the phytoplankton population.

Zooplankton and Phytoplankton in the Fall Cruise, November 7–10, 1955.

The collections taken in November present a picture of the abundance of plankton in the central and northern regions of the Strait. Since the data were taken only during the daylight period they do not give a true quantitative value, but only an approximation of the abundance of plankton in November. Except for a region of moderate concentration (Fig. 9) at the boundary of the central and southern regions of the Strait (Stations 7A, 8A, 9A, 10A, and 11A) and three widely separated localities of moderate concentrations (Stations 18A, 19A, 20A,

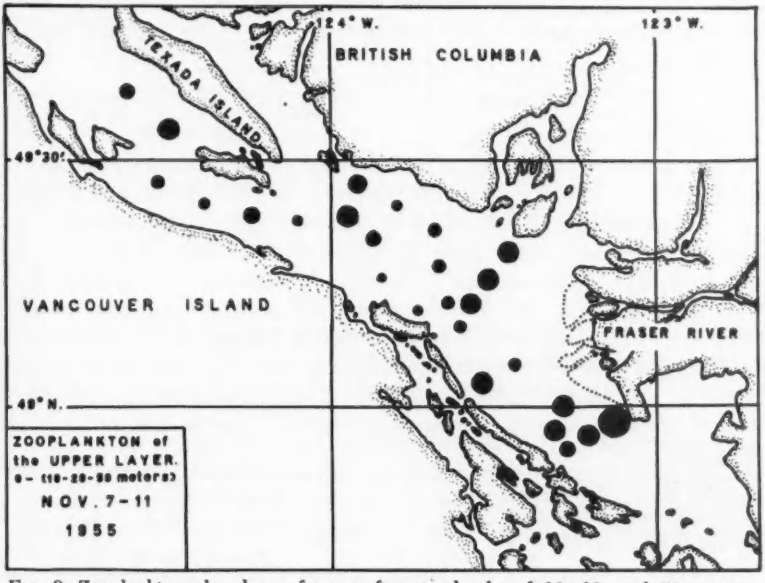

Fig. 9. Zooplankton abundance from surface to depths of 10, 20, and 50 metres, November 7–11, 1955.

30A, and 36A) the area of the Strait covered in November supported only a low concentration of zooplankton. It has already been pointed out that the water reaches an almost homogeneous state in the autumn with colder temperatures than in June and a small salinity gradient. These two factors are assumed to be limiting in November. The region of moderate zooplankton concentration corresponds to the zone of greater fresh water and sea water admixture off Point Roberts where a high salinity gradient exists in November.

The centre of abundance for the copepods was in the 50–0 metre zone. Among the copepods, the juveniles of *Calanus finmarchicus* and *Pseudocalanus minutus* were predominant in 20–0 metres at Stations 7A, 8A, 9A, 10A, 11A, 15A, 18A, 19A, 20A, 26A, 28A, 30A, 31A, 33A, 35A, and 36A, while the adults of *Calanus finmarchicus, Corycaeus affinis, Pseudocalanus minutus, Paracalanus parvus, Tortanus discaudatus,* and *Acartia longiremis* were predominant in 50–0 metres in the area. The copepod association, with *Calanus finmarchicus* and *Pseudocalanus minutus* as predominant representatives, must play an important role in the surface economy of the Strait in November.

No juvenile euphausids were caught in November and adults were found almost exclusively in the deeper hauls. The adults dominated the catch at Station 37A.

Chaetognaths and amphipods were found in small numbers at almost every station in the deeper hauls and on a few occasions in 50–0 metres.

Diatoms were so sparse in November as to be almost insignificant. Stations 28A, 34A, 36A, and 37A supported low concentrations of *Chaetoceros concavicornis. Coscinodiscus wailesii* was common at most of the stations visited in November.

DISTRIBUTION OF THE PLANKTON

Vertical Distribution

In comparing the abundance of the different groups of plankton in the upper 50 metres from one area of the Strait to the other, the problem of vertical distribution arises. The relative abundance of the different groups may vary depending on whether the sample came from 10–0 metres, 20–0 metres, 50–0 metres or deeper. At Station 25, for example, where hauls were made at 10–0, 20–0, and 50–0 metres, eggs were predominant from 10–0 metres, copepods from 20–0 metres, and juvenile euphausids from 50–0 metres. In order to study the vertical distribution, copepods were selected because they were the most important representatives of the plankton and contributed many species to the community. Analysis of samples containing copepods shows that these animals fall into three distinct groups:

1. the surface forms,
2. the subsurface forms,
3. the deep forms.

When a species is common in the deep as well as in the shallow hauls, it can be said that this species inhabits the surface layer. On the other hand, if a species

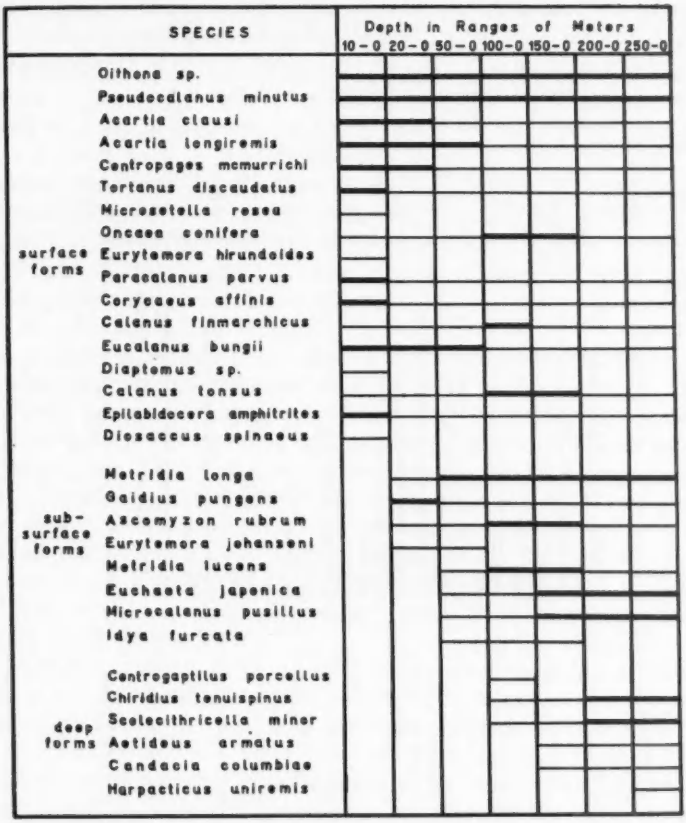

FIG. 10. Histograms showing the occurrence of copepods at different depths, June 8–16, 1955. (The heavy lines indicate the zones of maximum abundance.)

is never caught in the shallow haul and is abundant in the deep hauls, it is recognized as a deep form. When we compare the abundance of one species at different depths, its vertical distribution can be determined within narrow limits (Fig. 10).

Species such as *Acartia clausi*, *Acartia longiremis*, *Centropages mcmurrichi*, *Paracalanus parvus*, *Tortanus discaudatus*, and *Epilabidocera amphitrites* inhabit the surface layers (10–0, 20–0, and 50–0 metres), while *Microcalanus pusillus*, *Euchaeta japonica*, *Scolecithricella minor*, and *Chiridius tenuispinus* live in the deeper layers (250–0 metres).

Other groups of animals in the plankton also seem to follow a similar pattern of distribution. Euphausids as a group are represented by several larval stages.

The nauplii and metanauplii were generally abundant at 10–0 metres, while the calyptopis, furcilia and cyrtopia stages were found deeper. Juvenile *Calanus* were abundant at Stations 12 and 35 in the upper 20 metres. *Oikopleura* was predominant at 10–0 metres, and was seldom found deeper.

Horizontal Distribution at Constant Depth

Variations in abundance at constant depth for June 8–16 are demonstrated by the histograms (Fig. 11). The total zooplankton values are plotted in numbers per cubic metre. The shaded portion of the histograms represents the number of

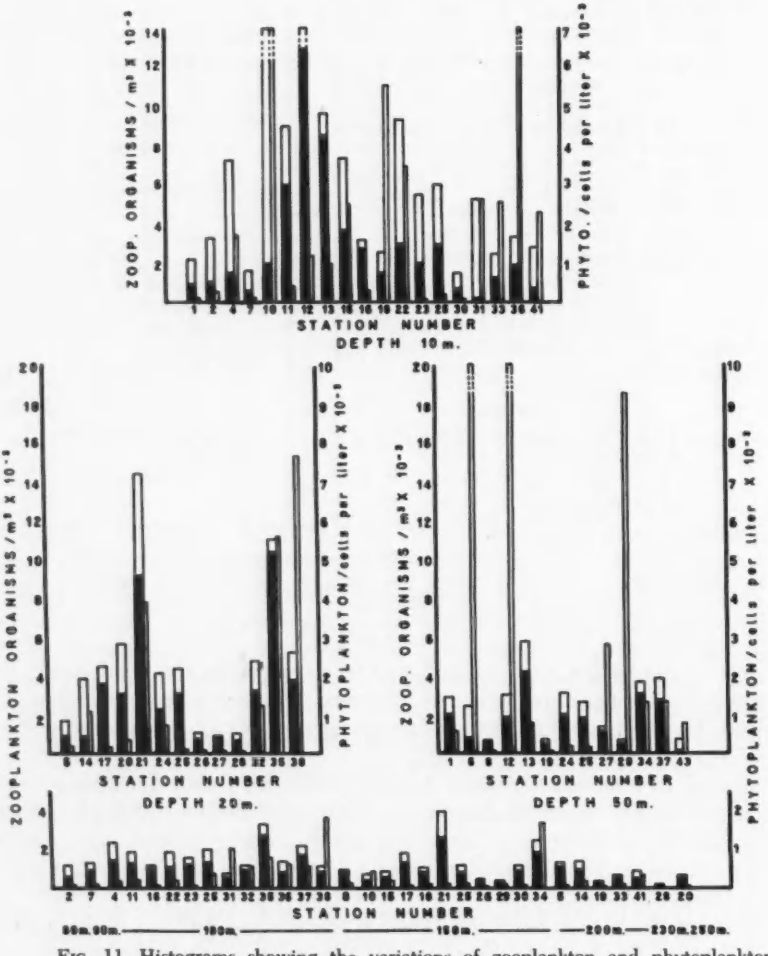
ZOOP. ORGANISMS / m³ X 10⁻³
PHYTO. / cells per liter X 10⁻³
STATION NUMBER
DEPTH 10 m.
ZOOPLANKTON ORGANISMS / m³ X 10⁻³
PHYTOPLANKTON / cells per liter X 10⁻³
STATION NUMBER
DEPTH 20 m.
ZOOP. ORGANISMS / m³ X 10⁻³
PHYTOPLANKTON / cells per liter X 10⁻³
STATION NUMBER
DEPTH 50 m.
STATION NUMBER

Fig. 11. Histograms showing the variations of zooplankton and phytoplankton at constant depths, June 8–16, 1955.

copepods in the catch and the narrow column to the right shows the volume of diatom cells per litre present in the same plankton sample.

At 10–0 metres, all stations but two (Stations 7 and 30) have concentrations higher than 2,000 animals per cubic metre; seven display concentrations ranging from 2,000 to 4,000 animals (Stations 1, 2, 16, 18, 33, 36, and 41); three more exhibit numbers of the order of 4,000 to 6,000 animals (Stations 23, 25, and 31), and seven have higher concentrations (Stations 4, 10, 11, 12, 13, 15, and 22). An inverse correlation exists at 13 out of 19 stations, between zooplankton quantities and diatom volumes. Where high blooms of diatoms occur, such as at Stations 10, 18, 33, 36, and 41, the number of animals is low. Station 12 has a very large number of animals and a low diatom population. Low diatom concentrations are also found at Stations 1, 2, 7, 11, 12, 13, 16, 23, 25, and 30.

The situation is somewhat different at 20–0 metres. Stations 5, 26, and 28 have concentrations below 2,000 animals per cubic metre; Station 14 shows a value of 2,800 animals per cubic metre; Stations 17, 20, 24, 25, 32, and 38, have values ranging from 4,000 to 6,000 animals; and Stations 21 and 35 have over 10,000 animals per cubic metre. An inverse relation between zooplankton and phytoplankton is apparent at Station 38 where diatoms predominate and zooplankton counts are low. The number of animals increases markedly at Station 35, near by, where diatoms are less numerous. At Stations 5, 17, 20, 24, 25, 26, 27, and 28, diatom volumes are low. Much higher counts are recorded at Stations 21 and 35. At this depth copepods still form the major part of the catch, as shown at Stations 17, 25, 32, 35, and 38.

At 50–0 metres only Station 13 had a concentration exceeding 4,000 animals per cubic metre; seven exceeded 2,000 (Stations 1, 6, 12, 24, 25, 34, and 37) and five had less than 2,000 animals per cubic metre (Stations 8, 19, 27, 29, and 43). Station 6, which exhibits the highest diatom concentration is located off Point Roberts, a region of relatively great turbulence. Moderate diatom concentrations also occur at Stations 12 and 29. Oikopleura sp. dominated the catch at Station 6, eggs and euphausids were found to predominate over copepods at Station 13. At all other stations copepods were always the dominant group of animals at 50–0 metres.

Greater depths do not need to be considered in detail. It is evident that quantities decrease very rapidly below 50 metres. All stations but five have concentrations below 2,000 animals per cubic metre. The other five stations (4, 21, 34, 35, and 37) have values ranging from 2,000 to 4,000 animals per cubic metre.

Applying the same analysis for the lighter November catches, a similar type of distribution is found (Fig. 12).

At 10–0 metres a higher concentration of animals per cubic metre is found than at any other depths, and copepods predominate. At 20–0 and 50–0 metres copepods are still the predominant form, but the relative concentrations of animals are much smaller. Below 50 metres, where mature individuals aggregate, catches are very small, except for chaetognaths, euphausids, and amphipods. Diatom volumes are so small in November that they do not appear on the histograms.

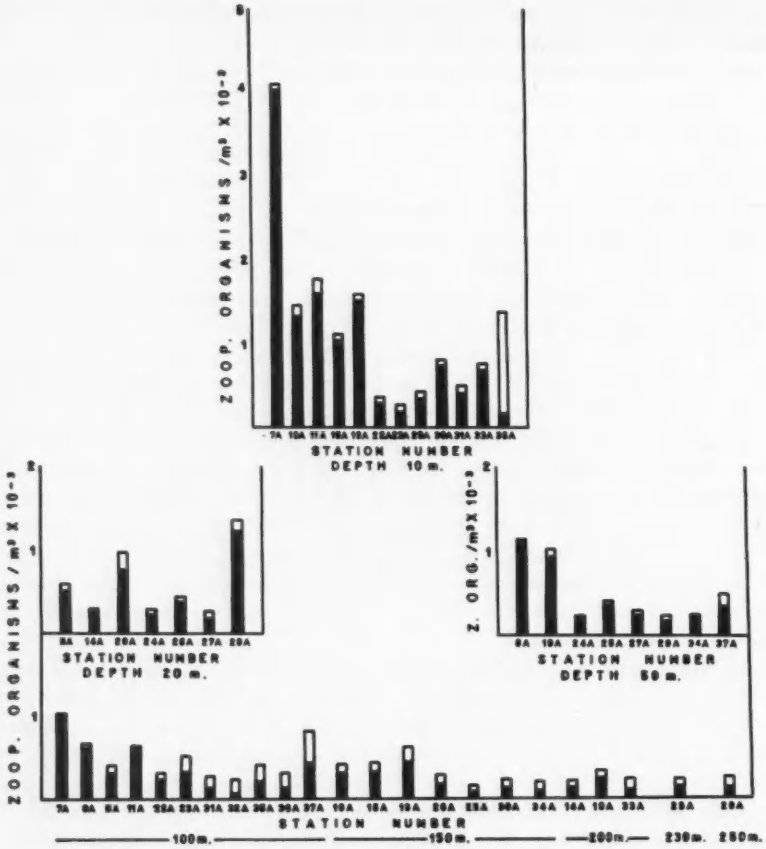

FIG. 12. Histograms showing the variations of zooplankton at constant depths, November 7–10, 1955.

SOME CHARACTERISTICS OF THE MOST IMPORTANT GROUPS

COPEPODS

Copepods formed the main bulk of the zooplankton. In June *Pseudocalanus minutus, Acartia longiremis,* and *Oithona helgolandica* contributed 65% of all copepods. They were supplemented by *Calanus* sp (15%), *Metridia longa, Eucalanus bungii* (5% each), *Metridia lucens* and *Centropages mcmurrichi* (3% each). Other species contributed 2% of the total catch.

In November *Pseudocalanus minutus, Oithona helgolandica,* and *Calanus finmarchicus* formed 77% of the total number of copepods. Next came *Metridia lucens* (10%), *Scolecithricella* minor (2%), *Microcalanus pusillus* (2%), *Corycaeus affinis* (2%), *Acartia longiremis* (2%), *Paracalanus parvus* (1%), and *Euchaeta japonica* (1%).

The following summarizes the features of the species regarded as most significant. Little attention is given to the rarer species which must have some importance but contributed little to this study.

PSEUDOCALANUS MINUTUS. The commonest species in June and November has a universal distribution in the Strait of Georgia. It formed 29% of the total catch in June and 28% in November. The males were more abundant at the onset of breeding and their number diminished more rapidly than the females after the breeding season. In June several females were egg-bearing and 50% of the catch was made up of juveniles. No egg-bearing females were found in November.

ACARTIA. The genus *Acartia* has two representatives in the Strait of Georgia: *A. longiremis* and *A. clausi*. The former is by far the most abundant. It shows wide fluctuations in abundance, thus 18% of the catch taken in June and 2% in November. The abundance of *Acartia* in June corresponded to the peak of main increase in the Fraser discharge. During June, males and females shared the catch in fairly uniform numbers, 25% for the males, and 32% for the females. In November the females accounted for 80% of the catch, and the males for 14%. Only scattered animals of *Acartia clausi* were found.

OITHONA. This microcopepod has two representatives in the Strait of Georgia: *O. helgolandica* and *O. plumifera*. A representative sample from 100–0 metres indicated the following composition: *O. helgolandica*, 3 males, 66 females, and 4 juveniles; *O. plumifera*, 7 females. The former formed 18% of the catch in June and 25% in November. *Oithona* was found at all depths at all stations in abundance but with greater concentration in 50–20 metres.

CALANUS. Juveniles of this genus were very numerous. They accounted for 14% of the catch in June and 23% in November. The adults of *C. finmarchicus* were present at all but three stations and always in small numbers. A total of 13 males and 90 females were identified. *C. tonsus* occurred in much larger numbers. A total of 909 females were identified. Four immature females of *C. cristatus* were found in the Strait.

In November, only *C. finmarchicus* could be found. The juveniles were most abundant within the vicinity of the Fraser River.

METRIDIA. It is represented by *M. lucens* and *M. longa*. The males of *M. lucens* are less numerous than the females (193 males, 512 females) and are found in shallower water. In November the males were found at all depths. The females, on the other hand, were absent from the upper 50 metres. *M. lucens* is more numerous in the fall. It has two breeding seasons, one in the spring, and one in the fall. The spring spawning must take place quite early in the season in the Strait, since in mid-June only 16% of the species were made up of young. Breeding of this species was taking place extensively in November. The catch was as follows: 26% males, 33% females, and 41% juveniles.

M. longa was found in greater numbers than *M. lucens* in June, but was very rare in November.

EUCALANUS BUNGII. *E. Bungii* was found during the June cruise only. The catches were made up mostly of juveniles that live in the upper layers. The adult males and females were distributed from 50 metres downward.

CENTROPAGES MCMURRICHI. This calanoid was also common in June only in the Strait of Georgia. *C. mcmurrichi* can apparently tolerate wide ranges of fluctuation in salinity, as shown by its presence in waters of salinity as low as 2‰, and as high as 20‰, and also by the fact that heavy breeding was taking place in parts of the Strait having a salinity less than 10‰. Twenty-four per cent were males, 19% were females, and 57% were immature. In regions of very high phytoplankton concentrations, this species of copepod was less abundant, where there was a very low concentration of diatoms the concentration of *C. mcmurrichi* was low. It seems then that the species needs a supply of diatoms high enough to provide ample food, but not so high that it may cause exclusion. The young of the species were most abundant in 20–0 metres, and the adult a little deeper (Table II).

TABLE II. Numbers of juvenile and adult *Centropages mcmurrichi* taken at 10–0, 20–0, 50–0, 100–0, and 150–0 metres, June 8–16, 1955.

	Depth in ranges of metres				
	10–0	20–0	50–0	100–0	150–0
Juveniles	68	107	111	143	69
Adults	41	70	93	93	80

Among the species encountered occasionally but never in abundance, in the plankton samples were: *Oncaea conifera, Scolecithricella minor, Microcalanus pusillus, Corycaeus affinis, Euchaeta japonica, Pracalanus parvus, Tortanus discaudatus, Epilabidocera amphitrites, Gaidius pungens, Chiridius tenuispinus*, and a few other. The species not listed were represented by only a few scattered individuals.

ONCAEA CONIFERA was found at all depths, but never in abundance in hauls taken shallower than 100 metres. Ten males and 90 females were counted from 33 stations in June. All the males but one were found attached to the females. In November 25 females were noted at 16 different stations, but no males were found.

SCOLECITHRICELLA MINOR was found only occasionally in June, but frequently in November. In June neither adults nor young were found shallower than 50 metres but both were present in the deeper hauls. In November both adults and young were found at all depths. Juveniles accounted for 45% of the catch, adult males 15%, and adult females 40%.

MICROCALANUS PUSILLUS was present in June at two-thirds of the stations. Males formed 47% of the catch, and females 53%. *M. pusillus* was caught most commonly in the November hauls. The catch comprised 43% males, 56% females, and 1% young.

CORYCAEUS AFFINIS was more numerous and widespread in November than in June in the Strait of Georgia. In June it was taken in less than one-half of the tows and never occurred in any quantity. In November it was abundant at

several stations and present in more than two-thirds of the samples. All representatives obtained were adult and came from shallow depths.

EUCHAETA JAPONICA was present at half the stations in June. Males, females, and young were always found deeper than 50 metres and were never in large numbers. The males made 30% of the catch, the females 10%, and the young 60%. *E. japonica* was found at all stations in November. The young were found in shallow water and the adults in deeper water. Males formed 16% of the total number, females 15%, and juveniles 69%.

PARACALANUS PARVUS. Very small numbers were counted in June. The species was found at almost every station in November although never in abundance. It usually occurred near the surface of the water. The females always outnumbered the males (93% against 7%).

TORTANUS DISCAUDATUS was never found in any quantity during this study. In the summer it was confined to the upper layers and in the autumn it was restricted to the area adjacent to the Fraser estuary. Only males (65%) and young (35%) were found in November.

EPILABIDOCERA AMPHRITRITES was found very infrequently in the summer, and always in small numbers. The catch was made up mostly of young (67%). In November only one individual was seen in all the samples studied.

GAIDIUS PUNGENS and CHIRIDIUS TENUISPINUS were rare in June and occurred in deep water. They were found in two-thirds of the hauls in November, but again in small numbers.

APPENDICULARIANS

OIKOPLEURA, the only genus identified, was of widespread occurrence in June (Fig. 13) and second in abundance only to the copepods. Larvae were taken in all shallow tows, sometimes far exceeding the copepods (Table I, Fig. 13). November hauls yielded only small numbers of *Oikopleura*.

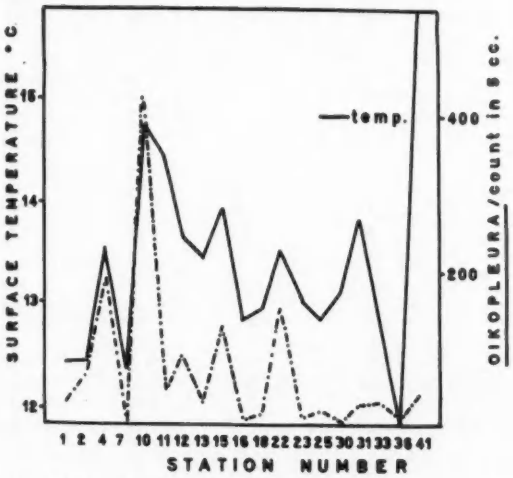

FIG. 13. Numbers of *Oikopleura* spp. found in the upper 10 metres plotted against surface temperatures, June 8–16, 1955.

EUPHAUSIDS

Developmental stages have been grouped as follows: (1) nauplii and metanauplii ("larval stages"); (2) all calytopia stages; (3) all fuarcili stages; (4) all cyrtopia stages; (5) adults. Euphausids were present at every station in at least some stage of development in June. Nauplii and metanauplii formed 9% of the catch, calyptopia 40%, furcilia 43%, and cyrtopia 8%, adults none. The two larval stages were concentrated in the upper layers, and older stages were more common in progressively deeper layers (Table III). No larvae were taken in November, but adults were moderately abundant, mostly at 100 metres and deeper (Table IV).

CHAETOGNATHS

Sagitta elegans, *Eukrohnia hamata*, and *Sagitta lyra* have been found. In June most of the population was concentrated in the upper 100 metres, and was

TABLE III. Larval stages, by numbers, of euphausids, June 8–16, 1955.

Stn. No.	Date	Depth (*m.*)	Nauplii and metanauplii	*Calyptopis*	*Furcilia*	*Cyrtopia*
1	June 13	10	—	1	—	—
1	,,	50	1	1	5	1
2	,,	10	1	4	1	—
2	,,	80	1	3	5	2
4	,,	10	4	1	—	—
4	,,	100	5	12	12	1
5	,,	20	—	1	2	1
5	,,	200	—	3	—	10
6	,,	50	—	35	—	3
7	,,	10	1	1	—	—
7	,,	90	—	1	—	1
8	,,	50	—	1	—	17
8	,,	110	—	1	13	9
10	,,	10	—	1	—	1
10	,,	150	—	4	2	1
11	,,	10	—	33	18	—
11	,,	100	—	44	20	11
12	,,	10	74	7	1	3
12	,,	50	3	3	4	1
13	,,	10	—	2	—	—
13	,,	50	—	9	17	12
14	June 14	20	4	1	2	1
14	,,	200	11	2	6	3
15	,,	10	1	1	1	—
15	,,	150	—	2	6	3
16	June 13	10	—	3	6	—
16	,,	100	—	13	8	25
17	,,	20	4	3	3	1
17	,,	150	5	8	18	12
18	June 14	10	—	18	5	1
18	,,	150	—	1	17	1
19	,,	50	—	7	—	1
19	,,	200	8	4	1	—
20	,,	20	4	10	5	2
20	,,	250	4	8	11	6
21	June 13	20	11	46	75	1
21	,,	150	7	133	160	21
22	June 14	10	3	16	6	—
22	,,	100	6	6	4	1
23	June 16	10	—	—	—	—
23	,,	100	2	—	—	—

TABLE III – continued.

Stn. No.	Date	Depth (*m.*)	Nauplii and metanauplii	*Calyptopis*	*Furcilia*	*Cyrtopia*
24	June 14	20	2	2	2	—
24	,,	50	3	9	5	—
25	June 16	10	1	1	2	—
25	,,	20	—	5	3	—
25	,,	50	1	13	12	—
25	,,	100	3	29	12	1
25	,,	150	5	42	41	1
26	June 14	20	—	—	1	1
26	,,	150	—	3	3	1
27	,,	20	—	—	1	—
27	,,	50	1	—	1	—
28	,,	20	—	2	—	33
28	,,	230	1	2	1	3
29	June 15	50	1	2	—	1
29	,,	150	—	1	2	1
30	June 14	10	—	8	2	1
30	,,	150	—	21	13	1
31	June 15	10	—	3	15	1
31	,,	100	—	29	11	1
32	,,	20	3	7	—	—
32	,,	100	2	6	—	—
33	,,	10	1	—	—	—
33	,,	200	4	25	84	2
34	,,	50	—	15	24	1
34	,,	150	—	26	65	1
35	,,	20	—	2	4	—
35	,,	100	1	37	39	3
36	,,	10	—	1	16	—
36	,,	100	—	57	91	3
37	,,	50	—	47	37	—
37	,,	100	—	45	50	—
38	,,	20	—	7	—	—
38	,,	100	—	3	2	4
41	June 8	10	1	1	2	—
41	,,	200	13	18	11	—
43	June 9	50	1	1	1	—

TABLE IV. Concentration of adult euphausids taken at different depths, based on a total count of the animals in each sample, November 8–11, 1955.

Depth (*m.*)	Numbers of adult euphausids (12 individual samples)											
	1	2	3	4	5	6	7	8	9	10	11	12
10	0	42	0	0	0	0	0	0	0	0	0	0
20	38	0	0	0	0	0	0	0	0			
50	94	0	8	0	0	0						
60	0											
65	0											
100	83	10	67	24	15	31	6	41	32	122		
110	103											
150	29	53	11	60	24	21	7	151				
200	24	46	22									
230	22											
250	152											

widespread throughout the Strait. *S. elegans* was most common. A few specimens of *E. hamata* were found mixed with *S. elegans*. Two specimens of *S. lyra* were taken in the deep hauls.

In November *S. elegans* was taken at every station and *E. hamata* was recorded at one station. Total counts taken in November indicated no immature individuals but several adults. These were present in all samples below fifty individuals but several adults. These were present in all samples below 50 metres (Table V) but were generally absent in samples from 10–0 and 20–0 metres.

TABLE V. Concentration of adult chaetognaths taken at different depths, based on a total count of the animals in each sample, November 8–11, 1955.

Depth (*m.*)	Numbers of adult chaetognaths (12 individual samples)											
	1	2	3	4	5	6	7	8	9	10	11	12
10	4	6	0	0	0	0	1	0	0	1	0	0
20	10	0	1	7	0	0	0	0	0			
50	16	10	15	5	1	43						
60	11											
65	7											
100	5	31	34	28	29	22	16	13	26	54		
110	16											
150	58	50	30	28	33	22	14					
200	20	36	23									
230	37											
250	50											

AMPHIPODS

The centre of abundance of immature forms was situated between 50–0 metres whereas the adults were located in deeper water (Table VI). 1.8% of adult amphipods were found at 65–0 metres and shallower, and 98.2% were obtained at 100–0 metres and deeper.

TABLE VI. Concentrations of adult amphipods taken at different depths, based on a total count of the animals in each sample, November 8–11, 1955.

Depth (*m.*)	Numbers of adult amphipods (12 individual samples)											
	1	2	3	4	5	6	7	8	9	10	11	12
10	0	1	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	3	0	0	0			
50	2	0	1	0	0	1						
60	1											
65	0											
100	11	16	10	10	21	14	2	0	0	126		
110	6											
150	35	15	27	15	14	35	7					
200	40	34	28									
230	41											
250	65											

GASTROPODS

Included here are the young gastropod larvae, the early clam larvae, and the pteropod larvae. Their main distribution is between 100–20 metres (Table VII). The group has been found at all depths outside these limits, but not in high numbers. Their distribution was ubiquitous in June and November.

TABLE VII. Vertical distribution of gastropod larvae and concentrations at each depth, June 8–16, 1955.

Depth (*m.*)	Number of larvae taken	Number of hauls made at each depth	Approximate number of larvae per haul	Percentage of the catch of larvae
10–0	19	19	1	2
20–0	71	13	6	6
50–0	123	13	9	11
100–0	407	14	29	37
150–0	316	11	28	29
200(+)–0	157	7	22	14

OSTRACODS AND CLADOCERANS

Ostracods were found at two-thirds of the stations in June. Only 5 of 123 mature individuals were caught above 50 metres. Ostracods were rare in November. Immature accounted for 40% of the total catch.

Cladocerans in June were living beneath the diatom population and in the region of maximum diatom concentrations. Only 11 individuals were found in November and all in the same haul.

LARVAE

Accounted for were copepod larvae, barnacle larvae and crab larvae. Most forms were abundant in June, but rare in November. As a rule, copepod nauplii and metanauplii appeared in greater numbers in 10–0 metres, barnacle nauplii somewhat deeper (50–0 metres), and cypris larvae of barnacles at 10–0 metres. Crab larvae were encountered much deeper. The zoeal stage was found rarely above 50 metres, and the metazoeal stage was centred in 100(+)–0 metres (Table VIII).

Other less frequent types of larvae included fish, shrimp, polychaete, coelenterate, holothurian, and many others. Few larvae were encountered in November.

TABLE VIII. Average numbers of copepod, barnacle, and crab larvae caught in each haul, June 8–16, 1955.

Depth (*m.*)	Copepod		Barnacle		Crab		
	Nauplii	Metanauplii	Nauplii	Cypris	Zoea	Metozoea	Megalops
10–0	9	4	2	1	1	1	1
20–0	5	5	3	1	1	1	1
50–0	12	8	6	1	1	1	1
00–0	7	8	3	1	1	1	1
00(+)–0	9	11	2	1	1	2	1

DIATOMS

The following nine species were most conspicuous, both in terms of abundance and regularity of occurrence in June: *Skeletonema costatum, Thalassiosira nordenskioldii, Nitzschia seriata, Rhizosolenia semispina, Biddulphia longicruris, Thalassionema nitzchioides, Chaetoceros decipiens, Chaetoceros affiinis,* and

Chaetoceros curvisetus. *Coscinodiscus wailesii* was the only genus commonly found in November.

SKELETONEMA. The genus is represented by only one species, *Skeletonema costatum*. No other genera of diatoms exceeded it in abundance in June. It occurred at all stations, and most of the time in very high concentrations. Not a single cell was encountered in the fall samples.

THALASSIOSIRA. The genus *Thalassiosira* is represented by three species: *T. nordenskioldii*, *T. rotula*, and *T. condensata*. *T. nordenskioldii* was second in abundance only to *Skeletonema costatum* in June in the Hardy Recorder hauls. It made up close to 50% of the total yield. All species of *Thalassiosira* were nearly always present in the vertical haul samples.

CHAETOCEROS. The three most abundant species were: *C. curvisetus*, *C. decipiens*, and *C. affinis*. *C. curvisetus* occurred at 80% of the stations. High concentrations of this species occurred in the central and northern regions of the Strait. *C. affinis* had a fairly similar distribution. Patches of *C. decipiens* appeared in the whole area of the Strait.

NITZSCHIA. *N. seriata*, and *N. pungens* attained numerical significance. The genus *Nitzschia* was found in large numbers, especially in the deeper hauls.

RHIZOSOLENIA. Representatives of this genus were found in abundance all over the Strait in June. One species, *R. semispina*, was very common, and another, *R. stolterfothii* was found occasionally. All other species identified (*R. hebetata*, *R. delicatula*, and *R. styliformis*) were not abundant.

BIDDULPHIA. The genus was abundant and was represented by three species: *B. longicruris*, *B. laevis*, and *B. aurita*. Of these, only *B. longicruris* occurred regularly and in June it reached very high concentrations.

THALASSIONEMA. *Thalassionema nitzschioides* was abundant and regular in distribution in June. It was present in more than two-thirds of the samples and had its maximum concentration off Point Roberts.

Figure 14 shows the percentage distribution at a depth of 10 feet, of the four predominant genera of diatoms along the Hardy Recorder cross-sections (Fig. 1). On the line A–B, values go on increasing from point Grey to Gabriola Island, but decrease slightly in the immediate vicinity of Vancouver Island. Along the line E–F, a slight increase is found south of Texada Island, but values go on decreasing northward. Along the line C–D, volumes of diatoms increase steadily southward until they reach their maximum opposite Point Roberts. They then decrease steadily in the last few miles of the section. Values obtained in the cross-section G–H, are much higher than those found on the line A–B.

CONCLUSIONS AND SUMMARY

1. During the summer when oceanographic conditions in the Strait of Georgia vary widely a great variety of organisms is found. During the autumn, when the waters reach an almost homogeneous state, the number and variety of

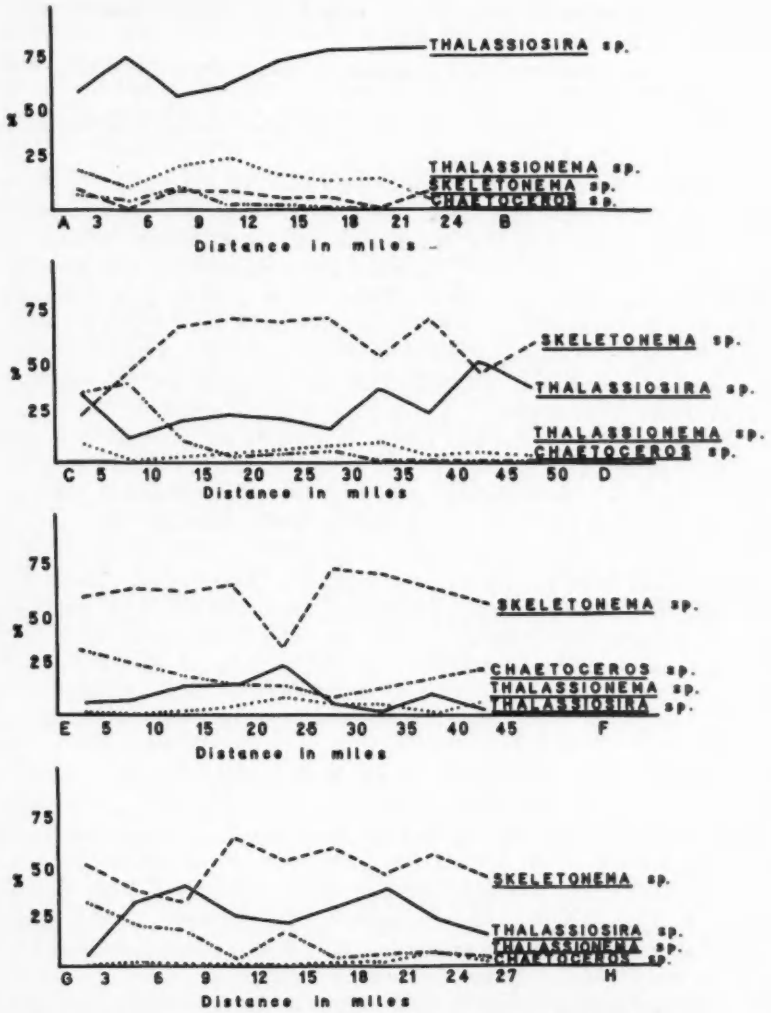

FIG. 14. Percentage distribution of the four most predominant phytoplankton genera along the Hardy Recorder cross-sections, June 8–16, 1955.

forms diminished considerably. In June, over 34 species of copepods, 45 species of diatoms, and 27 other groups of plankton organisms occurred in contrast with 21 species of copepods, 5 species of diatoms, and 19 other groups present in November.

2. Three centres of different concentration of zooplankton can be recognized and associated with the physical and chemical characteristics of the waters in the Strait of Georgia.

A) an area of high concentration with warm surface temperatures and strong mixing of water masses;

B) an area of intermediate concentration with colder surface temperatures and little mixing of water masses;

C) an area of low concentration with still colder surface temperatures and little mixing of water masses.

3. The number of diatoms found in June was low compared with the very high values known from some other areas of the world. The data suggest that the sampling may have preceded or followed a period of greater abundance. The waters north of the Fraser River contained large quantities of *Chaetoceros* and *Skeletonema* and those south of the Fraser River showed high quantities of *Thalassiosira* and *Skeletonema*. Few diatoms are taken close to the Fraser River estuary. The region is characterized by very low salinities and high turbidity.

4. Vertical distribution of zooplankton was apparent and the relative importance of the different groups of plankton organisms varied at 10–0 metres, at 20–0 metres, at 50–0 metres, and deeper. Copepods are grouped into surface forms, sub-surface forms, and deep-water forms. Many more species were found in the "upper zone" (50–0 metres) than at greater depth. Generally, the larval stages inhabited the first few metres and the adults lived at a greater depth.

5. Although the number of species of zooplankton and phytoplankton was large, only a small number of forms were dominant. The copepods *Pseudocalanus minutus*, *Acartia longiremis*, and *Oithona* sp. contributed 65% of all copepods in June; and *Pseudocalanus minutus*, *Oithona* sp., and *Calanus finmarchicus* formed 77% of the total number in November. Also the diatoms *Skeletonema costatum*, *Thalassiosira nordenskioldii*, and *Chaetoceros decipiens* always exceeded, by far, all other species in June, and *Coscinodiscus wailesii* was predominant in November.

6. The ratio of adult males to females was, in some copepod species, unequal in June and November, the males being more abundant at the onset of breeding but later diminishing in numbers more rapidly than the females after the breeding season.

7. Copepods generally formed the bulk of the zooplankton. They were very numerous in June, but the numbers decreased in November. When juveniles were very abundant the three dominant species (*Pseudocalanus minutus*, *Acartia longiremis*, and *Oithona helgolandica*) were responsible.

8. Appendicularians reached a peak in June in regions of optimum temperature for this group (12° C.). In such areas they far exceeded the copepod population and dominated the catch.

9. The population of euphausids is found to be distributed vertically according to age. There is a deeper distribution of the species as the larvae mature. Spawning takes place in late winter and early spring in the water of the Strait of Georgia.

10. Both juvenile and adult chaetognaths were present in the June catches. Immature forms were found in the supplementary hauls taken in 10–0 and 20–0

metres. Mature forms occurred in 50–0 metres and deeper. No larval forms were found in November.

11. The centre of abundance for amphipods lies between 50–0 metres in June and below 50 metres in November. The shallower June distribution is laid to the presence of several immature individuals.

12. Over 90% of the larvae caught in June belonged to three groups only: copepod larvae, barnacle larvae, and crab larvae. Copepod larvae were in the upper layer (10–0 metres), barnacle larvae were found somewhat deeper (50–0 metres), and crab larvae were encountered much deeper (100–0 metres).

13. Diatoms were most abundant around a depth of 10 metres. The western portion of the Strait supported a higher concentration than the colder, less saline eastern portion. The heaviest concentrations occurred a little south of the Fraser River estuary in an area of "steep" temperature and salinity gradients.

14. The euryhaline plankton organisms were found in great abundance during June and November 1955. Their distribution in the Strait of Georgia is only slightly affected by the oceanographic conditions because the fluctuations in the physical and chemical characteristics of the water lie within the limits of tolerance of the organisms. The stenohaline plankton organisms are limited to the more stable "lower zone". Within this "lower zone" the abundance and distribution of the stenohaline forms do not vary very much since temperatures and salinities are fairly constant in space and time. The euryhaline heliophilic forms (diatoms) are the most abundant. They are found in regions where fresh water originating from the Fraser River and saline water in the Strait mix. This mixing process favours phytoplankton abundance in at least two ways. The mixed waters may contain certain physical and chemical factors lacking in any one of the fresh and sea water masses alone. Also the entrainment of deeper saline water into the upper zone may bring up nutrients where they are available to phytoplankton.

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Some Considerations Concerning Sturgeon Spawning Periodicity[1,2]

By George Roussow[3]
Quebec Biological Bureau

ABSTRACT

In studying the age of sturgeons of the Danube (Romania), and of *Acipenser fulvescens* Rafinesque in the province of Quebec, I have observed a certain periodicity in their growth. This is seen not only in the age and length curves, but also in the cross-sections of the first ray of the pectoral fin which serve to determine the age of these fish. It is known that the growth of the body as a whole is in direct ratio to the growth of the bones, so the wide distance between two narrow (or winter) zones corresponds to the growth of the sturgeon during the summer. The growth retardations caused by the ripening of the gonads and the losses at the consecutive spawnings are visible in the ray sections in the form of "belts" of 2 to 7 narrower zones (or annuli). These indicate that the interval between spawning periods can vary from 4 to 7 years and more. It is noteworthy that spawning does not necessarily correspond with maturity, but may be delayed 2 or 3 years.

INTRODUCTION

While extensive study has been made of the various sturgeon species, particularly in the countries of Eastern Europe where their culture has been greatly intensified in the 20th century, there still remains a certain lack of definitive information concerning the periodic phases of their life story.

This lack is particularly marked when it comes to the study of Canada's eastern lake sturgeon, *Acipenser. fulvescens* Rafinesque, which increases the researcher's difficulties by its proclivity for spawning very late in life by comparison with other species. In fact this very proclivity is itself one of the main reasons for undertaking this research; for when a female fish has to reach in general the age of at least 16 years before reproducing its species there is an obvious danger of extinction—a matter of some grave concern as regards the St. Lawrence lakes. The more we know about this fish, the better we shall be able to help it hold its ground.

Of special interest is the spawning periodicity of this fish, a matter on which there still remains little positive agreement.

The present attempt to establish the spawning periodicity, together with other relevant data, has been undertaken on the basis of information read in the cross-section of the first ray of the pectoral fin.

The data given here came from research conducted during the summer of 1954, the autumn of 1955 and the spring of 1956 in the northern part of the province of Quebec. However, this research was based largely on my previous

[1]Received for publication September 28, 1956.

[2]The color plate illustrating this article has been supplied by courtesy of the Department of Fisheries of the Province of Quebec.

[3]Address: Quebec Biological Bureau, Université de Montréal, Montréal, P.Q.

J. Fish. Res. Bd. Canada, 14(4), pp. 553–572, 1957.
Printed in Canada.

studies on this same sturgeon in Lakes St. Louis and St. Francis of the St. Lawrence River in 1947 to 1949; also on studies of other species of surgeon of the Danube and Dneister of Romania in 1930 to 1939 and, as a student under Professor A. Borodin, of the Ural and Volga Rivers in 1916.

MATERIAL AND METHODS

As a staff member of the Biological Bureau of the Quebec provincial Game and Fisheries Department I was assigned to work on sturgeon research in that territory of the northern part of the province, where the Gold Belt Air Transport Company was doing a research fishery and the North Fish & Caviar Company is engaged in commercial fishing of sturgeon. These companies supplied me with all field facilities.

Work in 1954 was done at the following stations: Lake Matagamy; the mouth of the Olga River which connects this lake with Lake Olga; the Bell River from Cedar Rapids above the Kiask Cascades and Lake Taibi on the same river (but alse fed by the Indian, Sturgeon, Daniel Rivers and various brooks); also the Harrikana River. Gill nets of 4 and 10 inches (stretched) mesh were used for the more or less calm waters, and setlines carrying 400 to 1,000 hooks were used for rapids and turbulent waters. Several hundred sturgeon were captured. Of these, the sex of 96 fish was determined by dissection: 47 males and 49 females. Length (total) was from 28 to 53 inches; weight (living), 6 to 37 pounds; age was determined from 18 to 48 years. The greater average length of females may be accounted for by age difference; the males first come to spawn aged 8 to 13 years, the females at 16 years and more. All sturgeon were mature. These sturgeon of the northern part of the province were smaller for their age than those of the St. Lawrence River.

The work in 1955 also included some other lakes of the same territory. In September 1955 we captured sturgeon which were not migrating, but only "wandering", in Lake Olga. The 4-inch-mesh net in the channel between this lake and Goeland Lake took 52 young sturgeon, 23 to 35 inches in length (total). After measuring and removal of a slice of the first ray of the pectoral fin, all but 5 were tagged and released. These latter five were dissected to determine sex and condition of gonads; all were immature. All 58 sturgeon taken in the same channel with the 10-inch-mesh net were adult; length, 41 to 56 inches. The ovaries of the females showed which fish had spawned in the spring of the same year, which in 1954, in 1953, or even earlier; the more advanced ovaries had black eggs, to be spawned the subsequent spring-summer (1956). Male maturity was not so easily observed in the testicles.

In June 1956, the North Fish & Caviar Company fished the Ottawa River between Lakes Simard and Victoria. I was therefore able to obtain abundant material and attempt artificial fertilization of sturgeon eggs. This material is now being studied.

The observations made in June (the spawning season) in the Ottawa River give some indications on the spawning periodicity and on the composition of the migrating groups.

Sturgeon ascending from Lac Simard are stopped by the dam of the provincial power station at Rapid 2. Another dam of the same enterprise at Rapid 7 imprisons the sturgeon which are between the two dams; they cannot go to the upstream spawning beds.

So the sturgeon captured below Dam 2 and near the Kinojevis River, a feeder of the Ottawa River, can only have come from either Lac Simard or Lac des Quinze. It is here (below the dam) and on the Ottawa River spawning beds above the Kinojevis River that some 400 sturgeon were captured between May 30 and June 22.

In Carrière Bay only 4 sturgeon were captured between June 4 and 10. This would indicate that at that date the sturgeon were already migrating towards Rapid 16 and the Twin Rapids where they find good spawning conditions.

Altogether, at four fishing points (Rapid 2, Carrière Bay, Rapid 16 and Twin Rapids), four fishing teams (eight men in all) captured, between May 30 and June 22, 1,115 sturgeon having a total weight, dressed, of 9,950 lb. According to the statistics with which the company supplied me, this consisted of 3,061 lb. of "big" sturgeon (more than 12.5 lb. dressed); 3,117 lb. of "medium" sturgeon (8¾ lb. and more, dressed); and 3,772 lb. of "small" sturgeon (8 lb. and less, dressed). The "small" sturgeon were tagged and released. Taking into consideration the fact that the dressed fish, without head, fins and guts, weighs 43% less than the living sturgeon, it can be estimated that the captured sturgeon had a total weight of some 22,000 lb. and had an average weight of 20 lb.

With the assistance of Mr. Charles Prévost I was able to record the dimension, weight, age and state of gonads of 175 ♀ and 164 ♂ sturgeon; it was not possible to do the same for all the fish, because it was not feasible to execute the necessary manipulations while the sturgeon were being dressed on the tables provided for this purpose. After the age determination, and dropping cases of incomplete data, I was able to set up a table which will be given in this article.

From my observations in June 1956, during the spawning season, on the Ottawa River and the above-mentioned points, the following considerations arise:

According to the captures it can be noted that the sturgeon go upstream to spawn in groups composed of individuals in different states of maturity and of different ages and sizes.

The number of male and female spawners is about equal: 164 ♂ and 175 ♀.

The greater part of spawning in this region takes place between the end of May and the first three weeks of June (fishing was from May 30 to June 22). The water temperature during this period varies between 9° C. and 18° C.

It should be noted that on June 20 we captured a sturgeon below the Kinojevis River which we had already tagged; it was evidently on its way back to Lac Simard or Lac des Quinze.

The two sturgeon *morphae* (Roussow, 1955b), namely *A. fulvescens acutirostris*, the brown or lake sturgeon, and *A. fulvescens obtusirostris*, the black or rock sturgeon, were included in the catch, but no difference of age of maturity was observed in these two forms.

Measurements made were: total, standard and fork length; length and circumference of head; girth of body; distance from rostrum to barbels and barbels to mouth; length of all fins; number of dorsal, lateral and (where possible) ventral scuta; weight.

For age determination, a portion of the first ray of the pectoral fin was removed. Cross-section of this was made with a very fine saw, and sections 0.25 to 0.3 mm. in thickness were fixed to microscope plates with Canada balsam.

Age determination methods for St. Lawrence sturgeon, including study of otoliths, flat bones, cleithrum, first ray of pectoral fin, etc., have been described (Roussow 1955a). Here attention will be directed to some particular points in the study of the cross-section of the first ray of the pectoral fin. It may be remarked that not all fins of the sturgeon captured lent themselves to use of age determination methods.

A theoretical third indication, that of the flat bones (cleithra), which in the cross-section do indeed show marks corresponding to those in the ray section (Fig. 1), is neglected here for practical reasons. The flat bones are too thin and the preparation is too long to be suitable to our purpose. Also, in sturgeon as in other fish, they are subject to degeneration; it is baffling, when attempting a reading, to find a hole where there should be observable zones.

CONSIDERATIONS CONCERNING RAY SECTIONS

The essential point of this study is that the annual or seasonal zones on the cross-section of the first ray of the pectoral fin (which I may call the ray section) show a great deal more than just annual growth periodicity. They also show acceleration or retardation of the total growth of the fish due to other factors, especially when they are well marked and not obscured by secondary lines. These other factors include: migration and spawning periods, good or bad seasonal nutrition, individual wounds or illnesses[4], water temperature, floods and other water-level conditions, etc. (see also Cuerrier, 1951). These factors must all be taken into account when reading the ray section.

Sturgeon are often damaged when braving rapids and cascades to reach upstream places where spawning conditions are suitable, and ray fractures are frequent. Fins and rays will regenerate, but the regular growth, which is to say the formation of the seasonal zones, is disturbed. Thus a cross-section passing through a formerly fractured part gives an irregular figure from which it is impossible to determine age by counting seasonal zones (Fig. 2, 3). In such case a cross-section through the proximal part near but not including the fracture may permit age determination, but cuts made through parts distal to the point of fracture do not always give a sure configuration, since the growth of this part has not the normal regularity.

[4]I have noted a disease (epithelioma) of the sturgeon. Growth of the fish was definitely retarded by the tumor, and the retardation was clearly recorded in the ray section. The same was observed on sturgeon with ovarian cyst.

There is another way in which the place where the cut is made is important. The paired fins of the sturgeon form within two weeks of hatching. The pectorals can be observed as early as the 6th or 7th day. In a month the fry takes the form of the adult sturgeon except for juvenile proportions of the body—big head, pointed bony plates, etc. The first ray of the pectoral fin is well developed by the first winter and thereafter continues to grow. The alternation of winter inactivity and little feeding, and the contrary in summer, gives rise to the well known seasonal zones. These, in the reading of the cross-section, are found to be superimposed upon the other periodic patterns. The cut should be made at the proximal end, because the periodic rings become far less discernible as the distal end is approached. However, there is room for a certain amount of preference even here. Classen (1944) uses cross-sections made as close as possible to the articulation, obtaining thereby a plate which has a bifurcated aspect, due to the groove in the ray, in which the age is read in what we may call the branches (Fig. 4). However, I prefer to cut a bit more distally, where the picture is clearer, because I consider that a possible error of a year is of no great importance in sturgeon aged 10, 20 or upwards of 30 years (Fig. 5).

It may also be mentioned in these prior considerations concerning the ray section that the two rays following the first ray (these being situated as the base of, inferior to, the main ray) may also be sectioned as a control to the reading from the first ray, but adding one or two years. In certain cases, one of these secondary rays, or both, are not separated from the first ray but are enclosed within its rings (Fig. 6). For age reading in this case it is necessary to count the seasonal zones of the first ray up to the region where they begin to turn around the secondary enclosed ray, and then to follow the exterior bands which frame the zones of this secondary ray. However, only the first ray is concerned in the present study.

RAY SECTION AS THE FISH'S "CURRICULUM VITAE"

The big consideration is that the transverse section of the first ray of the pectoral fin can serve as the individual's "passport" or life story. This story, according to the present study, includes the following information concerning the fish: birth date and age; growth during favorable and unfavorable periods of particular years; age at which first reproduction took place; sex; and *the intervals between the spawning periods.*

The last is most important. Especially as regards the eastern Canada lake sturgeon, but also as concerns some other sturgeon species, the question has so far awaited a clear answer. Even the data by which the rather late maturation dates of our lake sturgeon can be fairly well established have hitherto been of an indirect nature, based chiefly on growth curves and the state of the eggs.

It is useful at this point to summarize the ages of maturity for different species and according to different authors.

Sturgeon reach maturity at the following ages, according to different authors:

FIG. 1. Flat bone (cleithrum) of a male sturgeon 23–24 years old.

FIG. 2. Section of first ray of damaged pectoral fin.

FIG. 3. Section of first ray of damaged pectoral fin. At left are seen the "belts" of the reproduction periods.

FIG. 4. Section of the proximal part of the first ray of the pectoral fin of an 11-year-old male sturgeon. The first "belt" is formed of 4 annuli.

FIG. 5. Section of the distal part of the first ray of a female. Some "belts" are formed after 17 years.

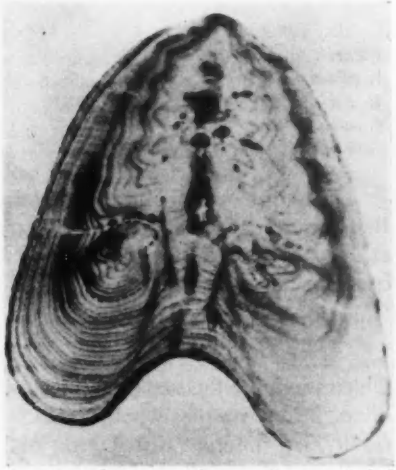


FIG. 6. A first ray with second ray included in it (left side, enclosed by the dotted line).

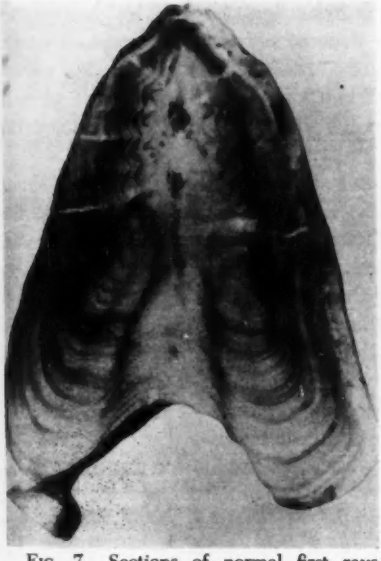


FIG. 7. Sections of normal first rays, showing successive "belts" of crowded annuli.

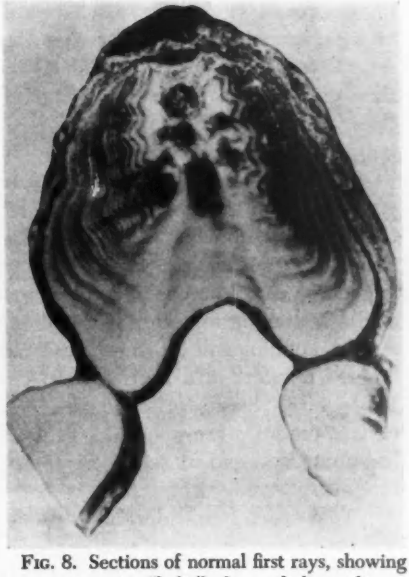


FIG. 8. Sections of normal first rays, showing successive "belts" of crowded annuli.

Species	Males	Females	Authors
A. fulvescens Rafinesque	14 years	23 years	Cuerrier, 1949
A sturio. Linné	7–9 „	8–14 „	Chalikov, 1949
A. güldenstädti Brandt	8–14 „	13–20 „	Lukin, 1949
A. baeri Brandt	10-12 „	12–14 „	Kozhin, 1949
A. ruthenus Linné	3–7 „	5–12 „	Lukin, 1949
Huso huso (Linné)	12–14 „	16–18 „	Chalikov, 1949

From my own observations in the province of Quebec, *Acipenser fulvescens* Rafinesque reaches maturity at 8 to 13 years, and spawning usually occurs first at 12 to 19 years for the male and 14 to 23 years for the female. This comes from counts made within the first ray of the pectoral fin, as described below.

READING AND INTERPRETATION OF RAY SECTIONS

Just as the sturgeon's year is divided into summer feast and winter famine, which produces the variation in ray structure recognizable as annuli, so its life is divided into post-spawning periods and pre-spawning periods, which might result in a different distribution of successive annuli. For the male fish loses more than one-tenth, and the female about one-fifth, of its total weight through discharge of milt or eggs. The production of this mass of vital substance, and the subsequent recuperation from spawning, may show up in both the growth curve of the fish and in the bones and ray sections (Negulescu, 1934).

Now, two definitions. To the nucleus or first seasonal zone I shall give the name of "central star". This is the beginning of the concentric annual feast-and-famine zones, or annuli, which establish the fish's age. After 10 or more years of wide spacing, the annuli rather abruptly become narrower and remain so for several years, forming a "belt" of closely-spaced annuli, which presumably reflect slow growth of the fish. Following the first belt there are several wide annuli, then a second narrow belt—the pattern being repeated several times in the larger fish.

To establish the significance of these belts in *Acipenser fulvescens*, I have given detailed consideration to the rays of 24 fish taken in June 1956, from the Ottawa River between Lakes Simard and Victoria. Tracings of the annuli (position of the winter growth) of these fish are shown in Fig. 9. Although it is, in general, easy to recognize the presence of the belts in these fish, the exact year of the beginning and end of a belt is sometimes difficult to decide. Fairly often a given annulus will be wide at one side of the section shown, and narrow at the other. The start of a narrow belt is usually better marked than is its end. In Table I the life-histories of the female fish are outlined, and some possible variant readings are given. In Table II a single best reading is selected for the beginning and end of each belt, sometimes rather arbitrarily, for the purpose of computing averages, etc.

There seems considerable *a priori* probability that the succession of narrow and broad belts of annuli would reveal the history of the fish's successive spawning periods, but it is not immediately clear at what stage the spawning act occurs. There are three possibilities: (1) It is possible that the narrow belts

TABLE I. Analysis of life histories of the 17 female sturgeon of Figure 9. (Upper Ottawa River between Lakes Simard and Victoria, June 1956.)

1. T.L. 30 in.; age 19 years (adult "virgin"), at first deposition of eggs. "Belt" begins to form at 13 years; is composed of 6 narrow zones. Not sticky but ripe.
2. T.L. 38.5 in.; age 20 years (almost ripe). "Belt" begins to form at 16 years and consists of 4 narrow zones.
3. T.L. 37 in.; age 26 years (not ripe). "Belt" is formed at 16 years and is composed of 7 narrow zones. Spawned at 23 years, and was captured at 26 years, when gonads were not yet ready for second deposition of eggs.
4. T.L. 39 in.; age 27 years. First "belt" formed at 16 years and consists of 4 narrow zones. Second "belt" formed at 25 years; composed of 2 narrow zones. Individual was captured upon arrival for second deposition with gonads ripe.
5. T.L. 43 in.; age 28 years. First "belt" formed at 13 years and has 5 narrow zones. Second formed at 22 years; 4 zones. This fish had spawned twice; was captured when arriving (not ripe), aged 28 years.
6. T.L. 44 in.; age 31 years (running). First "belt" begins at 13 years and is formed of 4 narrow zones; the second at 20 years has 5 narrow zones; third at 27 years has 5 zones and the fish (running) was on its way to deposit eggs for the third time.
7. T.L. 43.5 in.; age 32 years. First "belt" at 15 years, 3 zones; second at 21 years, 4 or 5 zones, third at 27 years, 3 zones. Fish was taken at age 32, mending from spawning 2 years previously.
8. T.L. 42 in.; age 32 years (not ripe). First "belt" at age 14 years, 4 narrow zones; second at 24 or 25 years, 5 or 6 zones. Spawned at age 30 and captured at age 32 years; eggs not ripe.
9. T.L. 44 in.; age 34 years (not ripe). First "belt" at age 16 years 3 or 4 narrow zones; second at 22 years, 3 or 4 zones; third at 29 years, 3 or 4 zones. Fish was captured at 34 years; eggs not ripe and no "belt" is apparent at the edge of section.
10. T.L. 43.5 in.; age 38 years (running); first "belt" formed at 15 years, 3 or 4 narrow zones; second at 22 years, 4 or 5 zones; third at 32 years, 6 zones. This female was completely ripe (running eggs); "belt" to edge of section.
11. T.L. 42 in.; age 37 years (not ripe; yellow eggs). First "belt" at 15 years, 3 or 4 zones; second at 28 years, 3 or 4 zones; third at 34 years, 3 zones, evidently incomplete.
12. T.L. 44.25 in.; age 38 years. First "belt" at 13 years, 4 or 5 zones; second at 23 years, 4 or 5 zones; third at 30 years, 5 or 6 zones; the last "belt" is followed by 2 wide annuli. Dissection revealed that the eggs were not ripe.
13. T.L. 48 in.; age 43 years. First "belt" formed at 13 years, comprising 6 zones; second at 21 years, 4 or 5 zones; third at 32 years, 3 or 4 zones; fourth at 40 years, 4 zones. This female had running eggs.
14. T.L. 45 in.; age 39 years (one or two years past spawning). First "belt" began to form at age 14 years, 5 narrow zones; second at 21 years, 4 or 5 zones; third at 34 years, 4 zones. This fish probably deposited eggs in 1955, or possibly 1954, to judge from the state of the ovary.
15. T.L. 53 in.; age 51 years. First "belt" at 11 years, 3 zones; second at 20 years, 3 or 4 zones; third at 32 years, 4 or 5 zones; fourth at 40 years, 4 zones; fifth at 47 years, 4 zones at edge of section. This female had running eggs, which were artificially fertilized.
16. T.L. 64 in.; age 58 years (small eggs). First "belt" at 12 years, 5 zones; second at 22 years, 4 or 5 zones; third at 34 years, 5 or 6 zones; fourth at 43 years, 5 zones; fifth at 52 years, 4 or 5 zones. One or two wider zones at the edge of the section. Eggs probably deposited the previous year; ovulae beginning to enlarge.
17. T.L. 55 in.; age 53 years. First "belt" at 10 years, 4 or 5 zones; second at 17 years, 3 or 4 zones; third at 22 years, 4 or 5 zones; fourth at 31 years, 5 or 6 zones; fifth at 39 years, 5 zones; sixth at 47 years, 4 zones. The last two annuli are wider; no ripe eggs.

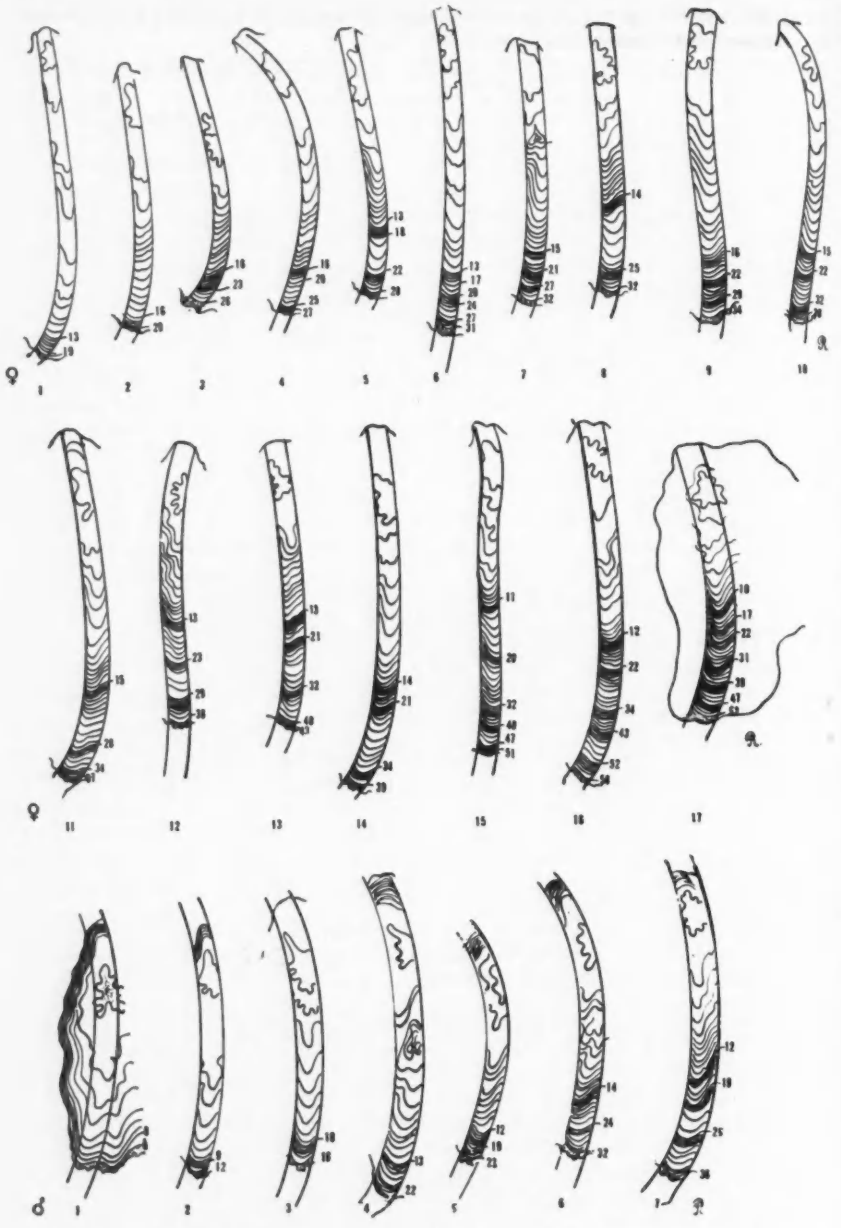


FIG. 9. Ray sections of 17 female and 7 male sturgeon sketched under a micro-projector. Only part of the section is sketched. (Upper Ottawa River between Lakes Simard and Victoria, June 1956.)

TABLE II. Identification of the most probable beginning and end of each of the belts of narrowly-spaced annuli, for the sturgeon of Figure 9. According to the interpretation suggested here, the start of a "belt" represents the beginning of several years of slow growth which accompanies maturation of the sexual products, and the last year in a belt is either the year of spawning or the year prior to spawning (see the text). Female fish which were ripe or nearly so when caught are indicated by (R). Bracketing of the final figures is a reminder that marginal annuli were not necessarily at the beginning or end of a belt: the last entry in each line is simply the age of the fish, in years completed.

Fish No.	First belt		Second belt		Third belt		Fourth belt		Fifth belt		Sixth belt		Seventh belt	
	Starts	Ends	Starts	Ends	Starts	Ends	Starts	Ends	Starts	Ends	Starts	Ends	Starts	Ends
Females														
1(R)	13	(19)												
2(R)	16	(20)												
3	16	23	(26)											
4(R)	16	20	25	(27)										
5	13	18	22	26	(28)									
6(R)	13	16	20	24	27	(31)								
7	15	18	21	25	27	30	(32)							
8	14	18	24	30	(32)									
9	16	19	22	25	29	32	(34)							
10(R)	15	18	22	26	32	(38)								
11	15	18	28	31	34	(37)								
12	13	17	23	27	30	36	(38)							
13(R)	13	19	21	25	32	35	40	(43)						
14	14	19	21	25	34	38	(39)							
15(R)	11	14	20	23	32	36	40	44	47	(51)				
16	12	17	22	26	34	39	43	48	52	56	(58)			
17	10	14	17	20	22	26	31	36	39	44	47	51	(53)	
Males														
1	(9)													
2	9	(12)												
3	10	15	(16)											
4	13	15	18	21	(22)									
5	12	19	(23)											
6	14	19	24	27	30	(32)								
7	12	15	19	22	25	29	33	(36)						

represent a post-spawning period of recuperation from the physical activity and interruption of feeding which characterize the spawning season. In that event each belt of narrow annuli would include a spawning year and the several years which follow it. (2) Equally, it is possible that a more rapid growth and maturation of ova and sperm cells during the years immediately before spawning, might make demands on the fish's metabolism such that body growth would be slowed down. In that event each belt of narrow annuli would *precede* spawning: spawning would occur during the last year of a belt of narrow annuli, or possibly in the first year of the subsequent series of broad annuli (if recuperation began during the same year after spawning). (3) Finally, both of the above periods may put strain on the fish, in which event spawning would occur somewhere in the middle of each belt of narrow annuli.

For a decision among the above possibilities, the annulus tracings of the 17 females in Fig. 9 may be compared with the description of the fish in Table I. It will be observed that in every instance where the female was mature or close to maturity when caught (so that it would spawn in the current year), the annulus sequence breaks off after a series of *narrow* annuli. This rules out alternative No. 1, above; that is, at least a part of each belt of narrow annuli must be assigned to the period immediately before spawning. However, there is still the possibility that slow growth may continue for a year or more after spawning. To check on this, the number of narrow annuli in the marginal belts of the ripe and almost-ripe females have been tabulated, as follows:-

Fish no.	Marginal narrow annuli
1	6
2	4
4	2
6	4
10	6
13	3
15	4
Av.	4.1

The average of these seven, 4.1 years, proves to be exactly the same as the average length of all the non-marginal belts of narrow annuli shown in the females of Fig. 9 (41 belts, av. length 4.1 years, range 3–7 years). Since the spawning occurs in June, this would suggest that rapid growth is resumed during that same year, right after spawning, in time to produce a broad annulus for that season. Because of the small number of ripe fish studied, sampling variability makes it impossible to be sure of this conclusion; and indeed it may seem unlikely that the fish could recuperate so quickly. But it is fairly certain that rapid growth (broad spacing of annuli) is normally resumed no later than the year following spawning.

On the basis of field dissections, I offer the following additional observations:

If there are no "belts" (e.g., No. 1, male) the fish is not adult. In the case of females without "belts" (No. 1, Olga, in 1955) the ovulae are seen at an early stage of development.

If the first belt is formed near the edge of the section and consists of more than 3 narrow zones, it is indicated that the fish (male or female) is proceeding to spawn for the first time.

In females in which the section shows a marginal first-time "belt" of only 2 or 3 narrow zones, the eggs *usually* are not completely ripe. If, on the contrary, there are more than three narrow zones constituting a marginal belt, the eggs are ripe and often running.

From the condition of the eggs it can be seen whether a "virgin" female is coming to spawn for the first time (ovaries full of ripe eggs), or is not yet adult. In either event the ovaries show no trace of the remains of eggs from a prior deposition.

If there are wider zones at the edge of the section following one or two belts from previous spawnings, the eggs are either unripe or incompletely ripe and would normally be deposited a year or two later. The same observations were made on sturgeon of the Abitibi lakes in 1954 and 1955.

In males this periodic regularity is less marked, but in the majority of cases, if the marginal belt is formed of 3 to 4 narrow zones the fish are adult and the milt is often running.

AGE AT FIRST SPAWNING, AND INTERVALS BETWEEN SPAWNINGS

Assuming, provisionally, that the last narrow annulus in each belt of narrow annuli marks the year of spawning, the distribution of ages at first spawning, and the intervals between spawnings, have been summarized in Table III, for the fish of Table II.

TABLE III. Frequency distributions of ages at first spawning, and of intervals between later spawnings, as indicated by the end of the belts of closely-spaced annuli on the fin-rays for the sturgeon of Figure 1.

Age (*years*)	Age of first spawning		Interval (*years*)	Intervals between spawnings						
				Males		Females				
	Males	Females		1–2	2–3	1–2	2–3	3–4	4–5	5–6
14	..	2	5	—	—	—	1			
15	3	0	6	1	—	4	1			
16	0	1	7	1	1	2	2	0	1	1
17	0	2	8	1	—	3	0	2	2	
18	0	5	9	—	—	2	1	1		
19	2	4	10	—	—	1	1	1		
20	—	2	11	—	—	0	0			
21	—	0	12	—	—	1	1			
22	—	0	13	—	—	1	3			
23	—	1								
Total fish	5	17	Total fish	3	1	14	10	4	3	1
Mean age	16.6	18.1	Mean intervals	7.0	7.0	8.2	9.5	8.8	7.7	7.0

The females spawned first at 14 to 23 years of age, average 18.1 years. Average intervals between subsequent spawnings were 8.2, 9.5, 8.8, 7.7 and 7 years. Out of 7 males shown in Figure 9, five (No. 3, 4, 5, 6 and 7) had spawned at least once. These matured first at 9 to 13 years and spawned at 15 to 19 years; subsequent spawnings occurred 7 years later on the average.

If the sturgeon recuperate quickly during the spawning year and put down a broad annulus then (cf. the previous section), the above ages at first maturity must be increased by 1 year. Another circumstance which could make some of the readings too low is that, as mentioned earlier, the ray section may in some cases have failed to strike the first annulus—particularly among older fish. Thus the Table III estimates of age at first maturity will tend to be too low rather than too high. However, the estimates of intervals between spawnings are not affected by either of these considerations.

CLASSIFICATION OF FISH ACCORDING TO GONAD CONDITION

Field dissections show that, mixed in among males and females whose sexual products are ready to deposit (females with running eggs are less frequent), there are many non-adult or unripe individuals, especially among the males.

It is a known fact in sturgeon culture that females (even when completely ripe) have a very short period in which the eggs are running hence ready to be deposited or to be artificially fertilized. It is likewise known that if the eggs are not deposited they enter into lipoid degenerescence or else begin to develop parthogenetically within the body of the female (Detlaf and Ginsburg, 1934; Eleonsky, 1936; Derjavin, 1922; and others). A problem in sturgeon culture is therefore that of having "running" females on the spawning beds. Males in the "running" condition are more frequent and the milt can be preserved in thermos bottles for some days.

Among the sturgeon captured between May 30 and June 22, 1956, I was able to examine 415 individuals while they were being dressed for commerce, to determine the state of their gonads and to sample their ovaries or testicles. Age was determined in 339 of these, 175 females and 164 males. But notes were taken on a much greater number at all four fishing points between the mouth of the Kinojevis River and Twin Rapids. In general, the numbers of males and females were about equal.

The number of sturgeon which had already spawned increased as the date advanced. The males in general are smaller, this being a matter of age since they come to spawn (or, if not mature, to accompany the group) at a younger age than the females. (The same observation was made by Derjavin (1922) for *Acipenser stellatus* of the Kura River.)

Males	Unripe	Ripe	Running	Spent	Degenerate or sick	
	24.2%	31.6%	20.6%	21.8%	1.8%	
Females	Unripe or "virgin"	Ripe	Running	Spent	Degenerate	Sick
	23.8%	26.7%	4.0%	38.3%	5.8%	1.4%

Note the big difference between the percentage of "running" males and that of "running" females. The age of the males varied from 8 to 45 years and their total length from 22 to 50 inches. The age of the females varied from 17 and 58 years; their total length from 28 to 64 inches.

AGE–LENGTH RELATIONSHIP

The curves of Figures 10 and 11 show the length distribution by age of *Acipenser fulvescens* from the northern part of the Province of Quebec. Near their left ends, these growth curves apparently reflect the periodicity of growth which has been described above. Among the females, especially, the initial sharp rise of the curve probably reflects the successive appearance, at first maturity, of specimens which have had increasingly long periods of rapid growth (before the onset of the first belt of narrow annuli); the plateau beyond, represented by few specimens, is the "catching-up" period prior to a new rise at about age 26, when the earliest spawners begin to appear for a second time. The alternation of rapid and slow growth may perhaps contribute to a waviness of the curve at older ages too.

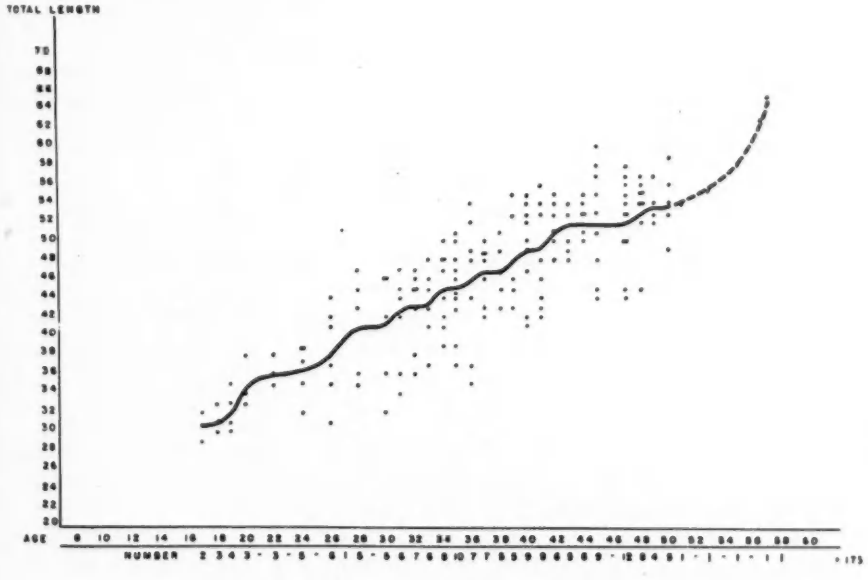


FIG. 10. Age–length graph of female sturgeon taken on the Ottawa River, June 1956.

The situation is less clear in respect to males (Fig. 11) probably because more non-mature males are taken, but the steep slope between ages 14 and 17 is suggestive.

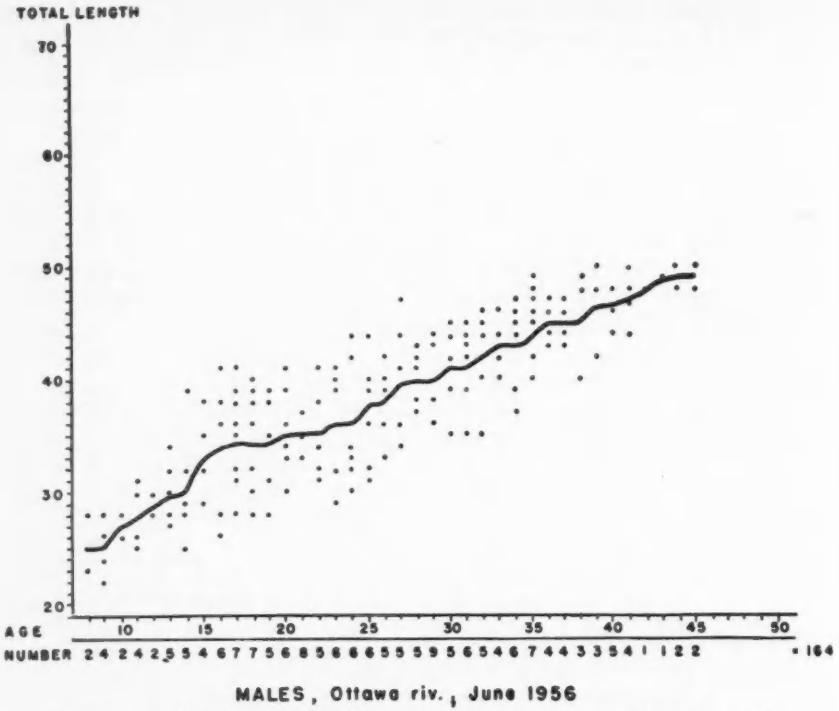


FIG. 11. Age–length graph of male sturgeon taken on the Ottawa River, June 1956.

Previous studies on sturgeon of the Danube (Roussow, 1937; Frecus, 1935), as well as on sturgeon of the St. Lawrence, show that their regular growth curve records a retardation during the intensive formation, and acceleration in the mending, of the gonads (see also the curves on pages 220–221 of Probst and Cooper, 1955).

STAGES IN EGG RIPENING

Another indication of periodicity of maturity is the state of the eggs, which, among other changes, go through a number of clearly marked stages between early formation and deposition.

As for the stages and states of the eggs, we may observe that before the first and subsequent spawnings there is a period of years between the early formation and the ultimate deposition of the eggs. During this period the eggs pass through various ripening stages and also, incidentally, they may pass through certain states such as lipoid degenerescence.

Age determination through examination of the eggs has been practiced for some time. Thus we find Derjavin, writing on *Acipenser stellatus* Pallas, observing in 1922:

"The male stellate sturgeon does not attain maturity before 8 years, oftener 12–15; the female not before 8 but generally at 14–18 years. The maturation of successive layings of eggs requires several years, perhaps five. The females when they enter the river have immature eggs, their maturation *being accomplished during their ascent to the spawning ground.* In very rare cases the eggs are not laid but undergo involution and absorption into the ovaries".

I give as an example a note on the development of the gonads in the alevins of the *Acipenser ruthenus* at 14 mm. The gonads at this time have the form of tiny ribbons covered with coelomic epithelium. Sex cannot be distinguished. In 35-mm. alevins (according to Detlaf-Bashmakow's citation of 1954) division of the sexual cells is not yet observable; in fact only at the age of 2 months (49 mm.) is the increase and division of cells to be observed. Only at the age of 1 year is the differentiation of the sexes observable; and in females of 18 months (220 mm.) the ovary is formed.

Three periods are noted in the development of the egg: division of the ovogonia, growth, maturation. The second period is responsible, more than the other two, for retarding growth.

I am giving a scale according to Detlaf and Ginsburg (1954) who have compiled data according to Lukin and Molchanova:

STAGES OF MATURITY (Lukin and Molchanova)

O. Ovaries and testicles in the form of transparent ribbon.

I. Ovaries white-yellowish (a few millimetres thick); eggs transparent, invisible to naked eye. Cells are polygonic in shape and are pressed close to the oviferous plaques. Rounded nucleus greater than the cytoplasm. On the cell edges are nucleoli. Cytoplasm granular. Diameter of ovulae 43–99μ and nucleoli 14–56μ. Fishes in this state have not yet deposited their eggs ("virgin").

II. Ovaries yellow. With ovulae characteristic of state 1, with larger white ovulae visible to naked eye. Oocytes of this state are oval and are pressed in the middle of the oviferous plaques. Their integument becomes follicular, composed of a single row of cells. Between the follicular membrane and the connective tissue is a membrane without structure. Diameter of ovulae: 284–397μ.

III. Ovaries yellow. Many white ovulae pressed closely together. Also observed under the microscope are little ovulae invisible to the naked eye. The ovulae are of sperical form. The nucleus spherical; the nucleoli on the periphery. Cytoplasm becomes granular (yolk appears); the grains occupy the central part but not in the region of the nucleus. The following layers are observed: near to the film no yolk; a very thin layer grains, then a layer of small grains; finally, around the nucleus, a zone free of yolk grains. In the film a *zona radiata* is observable. Diameter of eggs: 381–668μ; of the nucleus, 99–227μ.

IV. Nucleus spherical; in comparison with the cytoplasm, not very voluminous. Many spherical nuclei are deposited on the periphery in two or three rows. In the cytoplasm a superficial layer with pigmented (black) grains; a layer of small yolk grains; a zone of yolk grains occupies a large part of the cytoplasm; a small zone of small grains around the nucleus. Diameter of eggs: 1,029–1,645μ; of the nucleus, 185–355μ.

V. Eggs flowing.

VI. Eggs deposited. Ovary limp; with the naked eye can be seen small white ovulae of the subsequent reproduction (stage II), and the remains of pigmented (black) eggs.

The same authors give a classification according to Nedoshivin:

STAGES OF MATURITY (Nedoshivin)

O. Young. Sex not determinable by naked eye.

I. Sex determinable by the naked eye. Ovaries in form of pink ribbon differentiated in particles. Testicles in form of ribbons near the vertebral column.

II. Ovaries are developed but the eggs are not pigmented or enclosed in fat. Testicles wider than in stage I but very fine.

III. Eggs enclosed in fat and pigmented. Testicles in form red bodies.

IV. Eggs readily sifted (caviar). Testicles white.

V. Eggs and milt are flowing.

VI. Sexual products deposited.

Stage IV, above, can be divided into two: eggs readily sifted and eggs not passing a sieve.

According to my own observations on sturgeon, yet another state must be taken into consideration, that of non-deposited eggs; these either degenerate, or else they develop parthenogenetically up to the gastrula stage, or else they undergo a lipoid degenerescence or decompose by forming a grayish liquid upon which some eggs float (fishermen call this state "cement"). Naturally, these decomposed eggs are no good for either fertilization or for caviar.

I give sketches of fall-captured sturgeon ovaries (Fig. 12). Stages I and II are missing because our fishing methods do not allow us to take little sturgeon from 1 to 5 years old. I confine myself therefore to describing the more advanced stages. I insist that among the females taken on the spawning beds may be noted those which have deposited eggs and those lacking ripe eggs ("virgin").

Among females captured in 1954 and 1956 during migration, one particularly observes different phases of eggs; well pigmented and more or less ripe, which must be deposited in the next season[5], the undischarged eggs in a state of more or less pronounced lipoid degenerescence[6] and eggs without vitellin film and without chorion, the oocytes and oogonia of which look like poppy seeds.

These last-named must undergo a long ripening period. Also observed are females which have already deposited their eggs and have only a red-orange ovary with some grains of undischarged black eggs.

CONCLUSION

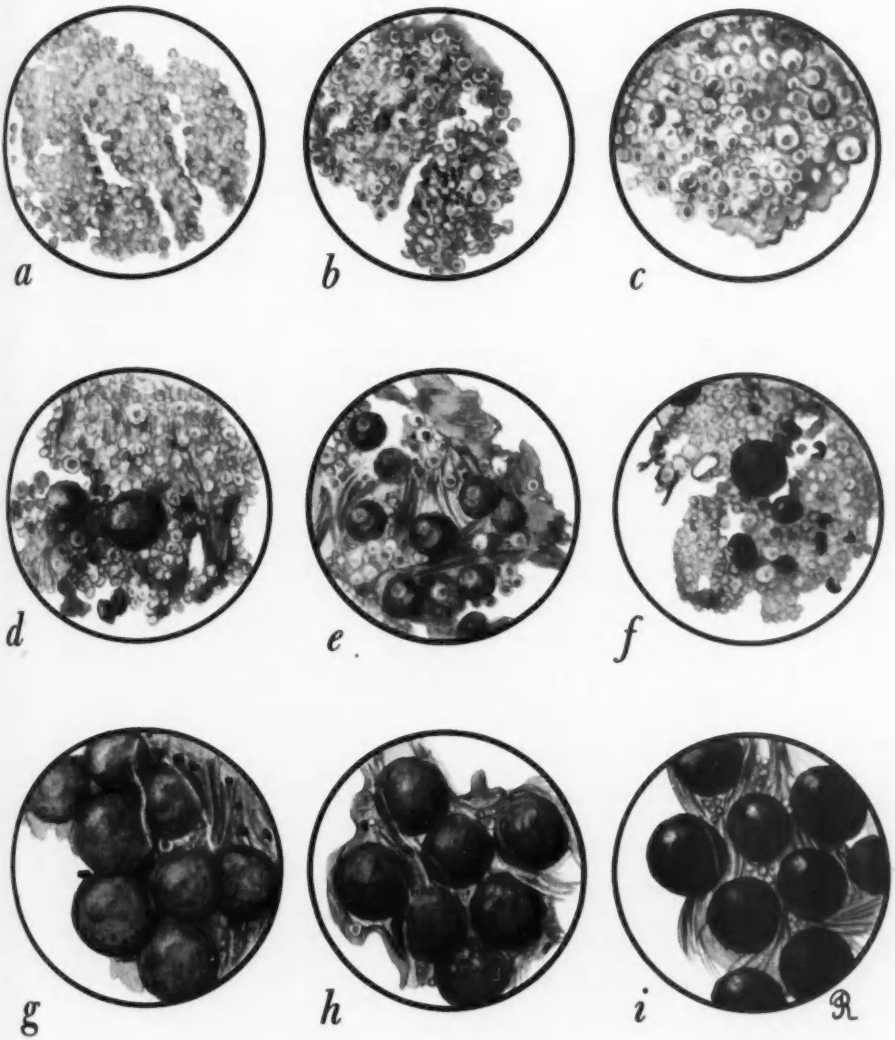
Direct observations, on-the-spot measurements at different seasons, and the reading of cross-sections of the first ray of the pectoral fin supply an indication as to the periodicity of the reproduction periods of the *Acipenser fulvescens* Rafinesque, which, by my estimation, varies between 4 and 7 years for the females. The formation of "belts", that is to say, of denser places in the seasonal zones, can give us an indirect indication as to this periodicity, which corresponds more or less to the state of the eggs and the fluctuations of the growth curves.

[5]These are the eggs which give the best caviar.

[6]These eggs give a caviar of inferior quality and its preparation calls for removal of fat.

LEGEND TO COLOUR PLATE OPPOSITE

FIG. 12. Stages in egg development: *a*, macroscopically observed white-rose ovulae; *b* and *c*, growth of eggs during 1–2 year period after age 15–17 years; *d* and *e*, further growth of eggs, now yellow in colour; *f*, same as *a* but just after spawning, when a few old eggs and some pigment still remain; *g*, eggs larger than in *e*, yellow; *h*, eggs brown, almost ripe, at times beginning to develop parthogenetically; *i*, eggs almost ripe but not yet running (good for caviar).



Georges Roussow
Department of Game and Fisheries
Province of Quebec

The formation of these "belts" (retardations of growth due to ripening of eggs and regeneration of lost weight) also supplies an indication that males mature at 8 to 13 years, females at 14 to 23 years. My direct observations on the upper Ottawa River between Lakes Simard and Victoria in June 1956, during the reproduction period of sturgeon, correspond to my previous studies. The material I am now analysing shows the same periodicity in the reproduction of *Acipenser fulvescens* in the northern part of the province of Quebec.

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Morphometric Comparison of Three Races of Kokanee (*Oncorhynchus nerka*) Within a Large British Columbia Lake[1,2]

By E. H. Vernon

British Columbia Game Commission and University of British Columbia, Vancouver, B.C.

ABSTRACT

Samples of kokanee (land-locked sockeye salmon) drawn from the spawning runs to seven streams tributary to Kootenay Lake, British Columbia, were compared statistically for morphological variation between streams, between lake areas and between years. Kokanee within three major lake areas displayed great similarity in age, size, vertebral count, scale characters and development of secondary sex characters. Samples from a representative stream of each area differed in age at maturity, size, growth rate in the first year, vertebral count, scale row count, gill raker count, head length of males, growth form of caudal peduncle, eye diameter, development of secondary sex characters, ova per unit total weight, and commencement of spawning period. Variation between years in size and vertebral count did not obscure or alter the stability of differences between races over a period of four years. Kokanee straying to spawn in areas not of their natal origin were identified by age, size, vertebral count, scale character, and scale row count, and totalled less than three per cent of 1,131 examined. Progeny of parents from the three races were propagated in a uniform environment from fertilization to six months after hatching. Parental differences in number of vertebrae were transmitted to offspring. Segregation during reproduction, due to strong homing tendencies, is considered the principal isolating mechanism leading to some genotypic divergence and considerable phenotypic variability.

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INTRODUCTION

Investigation of morphometric variation, particularly of meristic series, in wide-ranging species of fishes has in many cases disclosed a lack of homogeneity with respect to certain characters (Heinke, 1898; Schmidt, 1918; Hubbs, 1934; Lissner, 1934; Tester, 1937). By arbitrarily dividing the total range of a species

[1]Received for publication March 8, 1957.

[2]Partly based on a thesis accepted by the Department of Zoology, University of British Columbia, in partial fulfilment of the requirements for the degree of Master of Arts.

J. Fish. Res. Bd. Canada, 14(4), pp. 573–598, 1957.
Printed in Canada.

into several areas, greater homogeneity could be demonstrated within the resultant intraspecific groups. These relatively homogeneous groups, usually having rather ill-defined ranges, have been most commonly called races and have been considered to be partially isolated interbreeding populations. In recent years the existence of racial stocks within a large river system has been extensively used as a basis of conservation measures for sockeye salmon (*Oncorhynchus nerka*) of the Fraser River, British Columbia (Royal, 1953).

While the sockeye salmon of the North Pacific is usually an anadromous fish whose young remain in fresh water for at least a year, in many lakes non-anadromous populations of *Oncorhynchus nerka* live and reproduce entirely in fresh water. These fish have generally been known as kokanee to distinguish them from the anadromous form. Although no broad study of the comparative morphology of kokanee and sockeye has been made, no differences have been demonstrated, save the much smaller size and restricted migratory habits of the kokanee.

Ricker (1938) found that in Cultus Lake, British Columbia, some sockeye fail to migrate to the sea after the usual one or two years of life. These "residuals" could be differentiated at maturity from both sockeye and kokanee of the same lake. Ricker (1940) suggested that kokanee have evolved separately in many lakes from these residual off-shoots of sea-going sockeye. Foerster (1947) showed that kokanee raised in an inland hatchery from completely lake-locked stock and released as smolts in a coastal stream, migrated to sea and a few were later recaptured as typical mature sockeye.

Kokanee are isolated in lakes over a very wide area from Oregon to Northwestern Alaska as well as in Eastern Siberia and the Kamchatka Peninsula. Some evolutionary divergence might be expected to have occurred but only meagre descriptions are available and no evidence for divergence exists. Schultz (1935) described some body proportions of 58 kokanee from Lake Washington and Dymond (1936) described body proportions and meristics of two specimens from Christina Lake, British Columbia.

The present paper is a morphometric examination of spawning components of kokanee in a large lake. The purpose was to determine whether these were components of a single homogeneous population or whether kokanee within a large lake might be divided into discrete races spawning in separate areas. Kootenay Lake was chosen because it was known to contain large numbers of kokanee which spawned in several widely separated streams, and because impassable barriers prevent entry of anadromous forms to the lake. In addition to the examination of adult fish, rearing experiments were conducted to determine whether observed differences were genetic in origin or merely due to environmental effects.

EXPERIMENTAL AREA AND METHODS

Kootenay Lake

Lying in a deep glacial trench in southeastern British Columbia, Kootenay Lake is 65 miles (104 km.) long and 154 square miles (399 sq. km.) in area (Fig. 1). The main portion of the lake lies on a north-south axis, but the West Arm projects westward some 22 miles (35 km.). The lake is oligotrophic by

reason of the steep sides and uniformly great depth of the basin. For the purposes of this paper the lake is considered as consisting of three narrow arms radiating from the vicinity of Balfour. The North End extends from Balfour northwards and its limnology is greatly influenced by the large inflow of water from Lardeau River. The South End extends southward from Balfour and is greatly affected by the large discharge of Upper Kootenay River. The West Arm has a constricted entrance and a shallow sill in the vicinity of Balfour and extends westward to drain into Kootenay River.

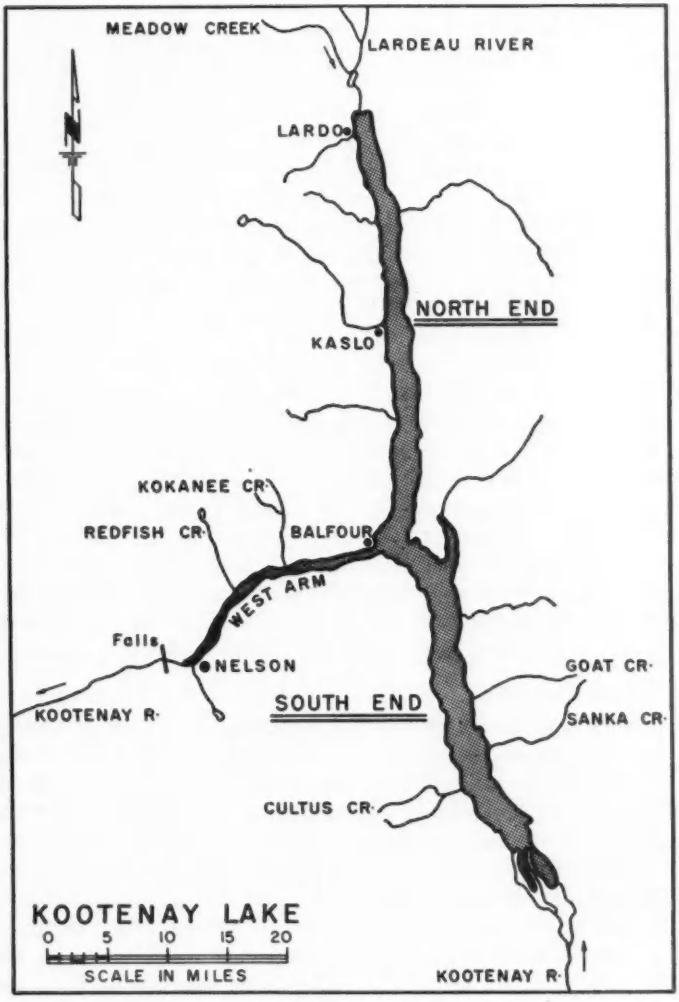

FIG. 1. Kootenay Lake.

Kootenay River drains into the Columbia River which in turn empties into the Pacific Ocean. Natural falls in Kootenay River have isolated Kootenay Lake salmon from anadromous stocks at least within historical times and probably for a much longer period.

Field Collections

Between August 30 and September 18, 1951, mature kokanee were collected from the spawning migrations to seven streams tributary to Kootenay Lake. Collections were made in Cultus, Sanka and Goat Creeks in the South End; Kokanee and Redfish Creeks in the West Arm; and Lardeau River and Meadow Creek in the North End (Fig. 1).

Between September 3 and September 16 in 1952, mature kokanee were collected from Goat Creek in the South End, Kokanee Creek in the West Arm and Meadow Creek in the North End. In September 1953, collections were made in Meadow and Kokanee Creeks. In September 1954, collections were made in Meadow, Kokanee and Sanka Creeks for experimental rearing. These are described in a later section.

Although various methods of capture were considered and tried and due thought given to the possibility of sample bias, it was found that a dip net was the only practicable tool in the turbulent streams of the South End and West Arm. To assure uniformity, this method was employed for all collections. The red coloration of males rendered them more easily seen and probably resulted in some bias toward their selection, but this would affect only the sex ratio of the collections.

It was not possible to collect fish throughout the spawning runs. To make samples representative of as large a portion of the runs as possible, fish were taken over a long section of some streams, on the assumption that fish in various parts of the stream had migrated at different times. In other streams, collections were made on more restricted sections but over a period of several days. In Goat and Sanka Creeks, two collections were made in 1951, nineteen and sixteen days apart respectively. Although in general, the fish collected are most representative of the early portions of the runs, comparison of early and late collections from Goat Creek indicate that this bias has no serious effect on the data.

Morphometric Procedures

To avoid possible errors in measurement due to differential shrinkage in formalin, all specimens collected in 1951 were photographed on a background grid of ten lines to the inch before preservation in formalin. Numbered tags were affixed to the specimens before photographing and these tags later identified each preserved fish with its respective photograph. All lineal measurements were made with calipers on the negative image projected to original size. In practice, this method was not altogether successful. Some measurements could not be made because of inability to distinguish accurately in the photographs the precise boundaries of various parts, for example, the origin or insertion of some fins.

In 1952 and 1953 the collections were preserved immediately in formalin. In 1954 only the parent fish for the subsequent controlled experiment were preserved

as specimens from their respective streams. Samples of progeny of these fish were preserved in formalin at two weeks and six months after hatching. To insure accurate vertebral counts, six-month-old fish were cleared in potassium hydroxide and ultra-violet light, stained in alizarin and fixed in glycerol.

Methods of measuring were as follows: head length, from tip of snout to posterior portion of operculum; peduncle length, from insertion of dorsal fin to posterior end of scale-bearing area; eye diameter, from anterior to posterior rim of orbit; gill rakers counted on excised left half of first gill arch with exclusion of two rudimentary rakers on the anterior ventral extremity. Vertebrae, exclusive of the hypural plate, counted on the exposed left side of column. No fused vertebrae were found. Pyloric caeca were removed individually as counted. Scale rows were counted four to six rows above the lateral line beginning at the gill cleft and terminating posteriorly with the last row which bissected the lateral line. Eggs were counted only if ovarian membranes were intact.

All specimens were sexually mature and resorption of scale margins was in some cases extreme, particularly in males. A comparison of scales from various body areas revealed excessive regeneration of scales posteriorly and excessive resorption anteriorly. Scales from the dorsum immediately posterior to the dorsal fin were found to be in the best condition and were used for age determination and scale measurements. Annuli were well defined in nearly all scales examined. Scale measurements were made with a microscope and ocular micrometer.

COMPARISON OF KOKANEE WITHIN AREAS

During collection of kokanee in 1951, size was strikingly uniform within various areas and differences between areas were equally as striking. Specimens collected in streams tributary to the South End were uniformly small. In two streams tributary to the West Arm, fish were consistently much larger, while in two streams of the North End they were intermediate in size. The red body and green head, typical male spawning coloration of kokanee (Schultz, 1935) appeared most highly developed in fish of both West Arm streams, while fish of South End streams were of a uniform dull olive grey. To investigate the apparent homogeneity of the kokanee which spawned in each arm of the lake, certain characters were examined in detail.

Age Composition

Table I gives the age composition of samples of kokanee from each of the Kootenay Lake streams. A single age class dominated the spawning component in each area in 1951. The predominant age of West Arm and South End fish was three years although a few males spawned at two years. Four-year-old fish formed the major portion of runs to North End streams with three-year-old fish present in insignificant numbers. Apart from the North End, four-year-old fish were found in only one stream—Goat Creek, in the South End, where they formed nine per cent of the collection. It will be shown below that these fish were almost certainly strays from the North End. For all comparisons in the following pages the dominant age group of each stream is used exclusively. Most fish younger than the dominant age group were males.

TABLE I. Age composition of spawning kokanee in streams flowing into Kootenay Lake, 1951. (A kokanee of age 2 is approaching the end of a 2-year life spawn, measured from the fertilization of the egg.)

AREA AND STREAM	AGE-GROUPS 2	3	4
SOUTH END			
Cultus Cr.	4	110	—
Sanka Cr.	2	76	—
Goat Cr.	6	155	16
WEST ARM			
Kokanee Cr.	4	70	—
Redfish Cr.	2	95	—
NORTH END			
Lardeau R.	—	2	100
Meadow Cr.	—	0	120

SIZE COMPOSITION

Table II summarizes the size distributions found in 1951. With the exception of Sanka Creek, where only 13 females were collected, all samples contain 26 of each sex chosen at random from the total sample of the predominant age class. No significant difference in size was found between sexes in any single sample, although males tended to be slightly larger in the group as a whole.

The size distributions exhibited no extreme departures from normality. Although differences between mean fork length for streams within the same area were in some cases significant ($P<.01$), these differences were numerically much smaller than differences between areas.

TABLE II. Size distribution of spawning Kokanee, 1951, of the dominant age in each stream. Spawning streams are indicated as follows: B = Goat Cr.; D = Cultus Cr.; E = Sanka Cr.; J = Lardeau R.; H = Meadow Cr.; F = Kokanee Cr.; G = Redfish Cr.

Fork length (*cm.*)	South End			North End		West Arm	
	B	D	E	J	H	F	G
16.0–16.9	3	2	1				
17.0–17.9	17	3	17				
18.0–18.9	29	23	14				
19.0–19.9	3	21	5	1	1		
20.0–20.9	—	3	2	4	6		
21.0–21.9	—	—	—	27	25	—	2
22.0–22.9	—	—	—	17	17	2	6
23.0–23.9	—	—	—	3	3	10	17
24.0–24.9	—	—	—	—	—	25	21
25.0–25.9	—	—	—	—	—	10	5
26.0–26.9	—	—	—	—	—	3	1
27.0–27.9	—	—	—	—	—	2	—
Total	52	52	39	52	52	52	52
Mean	18.19	18.78	18.22	21.73	21.40	24.66	23.75

NUMBER OF VERTEBRAE

Distribution of vertebrae counts are shown in Table III. The counts were made on the samples described in the previous section. The sexes did not differ significantly in number of vertebrae. At the 0.01 level of confidence, no significant differences in mean number of vertebrae were found between samples from the same area.

TABLE III. Distribution of vertebral counts of spawning kokanee, 1951.

AREA AND STREAM	Number of vertebrae 62	63	64	65	66	67	No.	Mean
SOUTH END								
Cultus Cr.	1	14	17	16	4	—	52	64.15
Goat Cr.	—	10	14	24	4	—	52	64.42
Sanka Cr.	3	7	14	14	1	—	39	64.08
NORTH END								
Lardeau R.	—	—	7	17	23	5	52	65.50
Meadow Cr.	—	—	—	20	24	8	52	65.77
WEST ARM								
Kokanee Cr.	—	2	16	20	14	—	52	64.90
Redfish Cr.	—	2	13	27	10	—	52	64.86

SCALE CHARACTERISTICS

Although quantitative comparisons were not made, marked similarity of scale pattern within areas was evident during examination of scales for age determination. Scales of West Arm fish were characterized by a very large area within the first annulus, while scales from South or North End kokanee had a much smaller area within the first annulus. Scales of North End fish were further characterized by a very narrow second annulus, occasionally being reduced to a single broken circulus. The uniformity of scale characteristics within an area was sufficient to enable the recognition, in a sample, of individuals from another area, i.e. only three scale patterns were observed and a kokanee outside its "home" area could be identified as such. Supporting evidence justifying this conclusion is given in a later section.

SCALE RESORPTION

Progressive resorption of scales with approach of sexual maturity is common among Pacific salmon. Correlated with this resorption is a thickening of the skin and an envelopment of the projecting portions of scales. These breeding modifications are most strongly developed in males. In the kokanee examined the dorsal and ventral scale margins were most extensively resorbed. In Kootenay Lake, the degree of dermal thickening and scale resorption was very similar in breeding kokanee within each area. It was moderate in both streams of the North End and extreme in both streams of the West Arm. On the other hand, kokanee from the three streams of the South End displayed very slight dermal thickening and scale resorption even in males which had completed spawning.

SUMMARY OF SIMILARITIES

In general, kokanee which spawn within the areas designated as North End, South End and West Arm display much greater homogeneity than do kokanee in Kootenay Lake as a whole.

Spawning kokanee in the North End are four years of age, display a characteristically narrow second scale annulus and moderate dermal thickening. Their mean fork length is approximately 21.5 cm. and mean number of vertebrae is 65.63.

West Arm kokanee spawn at three years of age, display a very wide area within the first scale annulus and extreme scale resorption and dermal thickening. Their mean fork length is approximately 24.5 cm. and mean number of vertebrae is 64.88. West Arm kokanee also develop a uniformly high degree of breeding color.

Finally, kokanee from the South End form a group maturing at three years of age, having a narrow area within the first scale annulus and very slight dermal thickening, scale resorption or breeding color. Their mean fork length is approximately 18.5 cm. and mean number of vertebrae is 64.22.

COMPARISON OF KOKANEE BETWEEN AREAS

The Samples

As shown in the previous section, examination of kokanee samples collected from seven streams tributary to Kootenay Lake indicated that considerable homogeneity resulted if the lake were rather arbitrarily divided into three major areas. This homogeneity was particularly evident with respect to size at maturity and number of vertebrae. While it might be desirable to examine samples from all streams in further detail, it was considered more profitable to compare samples of kokanee from one stream in each area, assuming each to be typical of that area. Fish from Cultus Creek in the South End, Kokanee Creek in the West Arm and Lardeau River in the North End were selected, examined and compared in more detail as representative of each area. Twenty-six of each sex were chosen at random from the predominant age group of the 1951 collections from each area, and these form the samples for all comparisons in this section.

Age and Size at Maturity

Whereas four-year-old fish comprised over 98% of the North End sample, South End and West Arm kokanee were predominantly three years old at maturity, this age group contributing 96.4% and 94.6% to the respective total collections (see Lardeau, Cultus and Kokanee in Table I).

Kokanee from each area formed very distinct size groups. The distributions of fork length are shown in Table IV. A comparison of variation in size within and between areas is made in Table VI. Differences between areas in mean fork length were significant ($P<.01$). Distributions of weight are shown in Table V. Differences between mean weights were also significant ($P<.01$). No statistically significant differences existed in mean weight or length between sexes.

Table IV. Distributions of fork length of Kokanee, 1951.

		Length range in centimetres											
Area	Mean	16.1–17.0	17.1–18.0	18.1–19.0	19.1–20.0	20.1–21.0	21.1–22.0	22.1–23.0	23.1–24.0	24.1–25.0	25.1–26.0	26.1–27.0	27.1–28.0
S. End	18.78	2	27	17	2								
N. End	21.73	—	—	—	1	8	29	11	3				
W. Arm	24.66	—	—	—	—	—	—	2	11	25	9	4	1

TABLE V. Distributions of weight of kokanee, 1951.

Area	Mean	Weight range in grams											
		<46	46–60	61–75	76–90	91–105	106–120	121–135	136–150	151–165	166–180	181–195	196–210	>210
S. End	57.9	3	32	16	1									
N. End	105.4	—	—	1	2	23	21	5						
W. Arm	158.2	—	—	—	—	—	2	4	16	13	8	5	3	1

TABLE VI. Differences in mean fork-length (in centimetres) within and between areas, 1951, with mean lengths in brackets. Differences to left of or below the double line are within the same area, those to right are between areas.

	South End		North End		West Arm	
	Sanka (18.22)	Cultus (18.78)	Meadow (21.40)	Lardeau (21.73)	Redfish (23.85)	Kokanee (24.66)
SOUTH END						
Goat (18.19)	0.03[a]	0.59	3.21	3.54	5.66	6.47
Sanka (18.22)	—	0.56	3.18	3.51	5.63	6.44
Cultus (18.78)	—	—	2.62	2.95	5.07	5.88
NORTH END						
Meadow (21.40)	—	—	—	0.33	2.45	3.26
Lardeau (21.73)	—	—	—	—	2.12	2.93
WEST ARM						
Redfish (23.85)	—	—	—	—	—	0.81

[a]A non-significant difference. All others are significant at the P = 0.01 level.

MERISTIC CHARACTERS

VERTEBRAE

The distributions of vertebral counts are shown in Table VII A. Differences in number of vertebrae between sexes were not significant, but differences between areas were ($P<.01$). Mean number of vertebrae was highest for North End kokanee followed by West Arm and South End fish. Table VIII shows the small differences within areas in comparison to the differences between areas.

Tests of significance for these analyses were based on the "T" and "F" distributions (Snedecor, 1946). To confirm that these methods were suitable for testing differences between vertebral counts with such restricted variability, a chi-square test based on marginal probabilities was applied to vertebrae data and led to the same conclusion as had application of analysis of variance. The chi-square value was 36.013 with 4 d.f. ($P<.01$).

TABLE VIIA. Frequency distributions of vertebral counts, 1951.

Stream	Area	62	63	64	65	66	67	Mean
Cultus Cr.	South End	1	14	17	16	4	—	64.15
Kokanee Cr.	West Arm	—	2	16	20	14	—	64.90
Lardeau R.	North End	—	—	7	17	23	5	65.50

TABLE VIIB. Frequency distribution of number of scale rows along the lateral line.

	Area	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	Mean
Cultus Cr.	South End	2	1	2	4	5	5	4	6	4	6	2	2	4	1	0	1	1	127.96
Kokanee Cr.	West Arm	—	1	—	2	9	5	8	5	4	5	8	2	2	1	—	—	—	128.06
Lardeau R.	North End	—	—	—	—	3	3	3	11	5	4	9	2	5	0	2	4	1	130.10

TABLE VIII. Difference between mean vertebral count within and between areas, 1951, mean counts in brackets. Mean differences to left of or below the double line are within areas, those to the right are beteeen areas.

	South End		North End		West Arm	
	Sanka (64.08)	Cultus (64.15)	Meadow (65.77)	Lardeau (65.50)	Redfish (64.86)	Kokanee (64.90)
SOUTH END						
Goat (64.42)	0.34	0.27	1.35[a]	1.08[a]	0.44[a]	0.48[a]
Sanka (64.08)	—	0.07	1.69[a]	1.42[a]	0.78[a]	0.82[a]
Cultus (64.15)	—	—	1.62[a]	1.35[a]	0.71[a]	0.75[a]
NORTH END						
Meadow (65.77)	—	—	—	0.27	0.91[a]	0.87[a]
Lardeau (65.50)	—	—	—	—	0.64[a]	0.60[a]
WEST ARM						
Redfish (64.86)	—	—	—	—	—	0.04

[a]Differences significant at the P = 0.01 level.

SCALE ROWS

The distribution of scale row counts are shown in Table VII B. No significant differences in mean scale row counts were found between sexes. North End kokanee had a significantly higher number of scale rows ($P<.01$) than did South End or West Arm kokanee. Differences between West Arm and South End fish were not significant.

The high scale row count of North End kokanee may be related to a greater number of somites as suggested by the high vertebral count of this group. However, close correlation of scale rows and vertebrae need not be expected invariably. Scale rows were counted four to six rows above the lateral line, and Neave (1943) has shown that a variable degree of branching may occur at this level.

GILL RAKERS

Table IX A shows distributions of gill raker counts. No differences were found between sexes in number of gill rakers. Gill raker counts of West Arm and North End kokanee were not significantly different but South End kokanee had a significantly lower gill raker count than either of the other two groups ($P<.01$).

It can be noted in Table IX A than mean number of gill rakers forms a progression (South End<North End<West Arm) which is superficially similar to that formed by size (Tables IV and V). However, gill rakers plotted against weight of individuals showed no correlation within areas and it was concluded that the lower number of gill rakers of South End kokanee was unassociated with the smaller size of these fish.

TABLE IXA. Frequency distributions of gill raker counts, 1951.

Area	31	32	33	34	35	36	37	38	Mean
South End	2	10	12	9	9	9	1	—	33.85
North End	—	1	4	14	8	20	5	—	35.10
West Arm	—	—	3	9	16	10	11	3	35.50

PYLORIC CAECA

Distributions of pyloric caecal counts are shown in Table IX B. No significant differences were found between males of each area or between females of the North End or West Arm. South End females were significantly lower in caecal count than North End or West Arm females and were also significantly lower than South End males ($P<.01$). The meaning of this difference is not clear. It is associated with a skewed distribution of caecal counts for South End females.

Caecal count plotted against weight of individuals within areas revealed no correlation. Over the size range studied there was no tendency for large kokanee to have more caeca.

TABLE IXB. Frequency distributions of number of caeca, 1951.

Group	50–54	55–59	60–64	65–69	70–74	75–79	80–87	Mean
S. End ♂	1	4	7	7	6	1	—	65.00
S. End ♀	8	8	4	4	2	—	—	58.50
W. Arm ♂	—	2	5	10	5	1	3	68.38
W. Arm ♀	1	2	7	10	2	3	1	66.15
N. End ♂	—	2	6	11	4	3	—	67.42
N. End ♀	—	1	8	9	5	3	—	67.19

RELATIVE BODY PROPORTIONS

All regressions were done on logarithms of body measurements

REGRESSION OF HEAD-LENGTH ON FORK-LENGTH

Samples consisted of 26 of each sex from each of the three areas previously discussed. Males had significantly larger heads than females in each area and therefore the sexes were compared separately. The adjusted mean log head-length (last row of Table X) of West Arm males was significantly higher ($P<.01$) than those of North End or South End males. The means of North End and South End male samples were not significantly different. No significant difference was found between adjusted mean head-lengths of female kokanee. The shorter heads of North End females approached the level of significance ($P<.05$) when compared with West Arm females, but no difference was evident between North and South End females or between West Arm and South End females.

TABLE X. The relation of head-length to body-length, 1951 kokanee.

Area	West Arm		South End		North End	
Sex	♂	♀	♂	♀	♂	♀
Number in sample	26	26	26	26	26	26
Mean log. fork length	1.3942	1.3898	1.2785	1.2681	1.3372	1.3361
Mean log. head length	0.7766	0.7215	0.6292	0.5735	0.6606	.06251
Regression Coefficient	0.9722	1.0872	0.7249	1.1063	1.0934	1.0410
	±	±	±	±	±	±
	0.1327	0.2881	0.1782	0.1417	0.1681	0.2320
Prob. of Regression = 0	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Mean log. head length at mean log. fork length = 1.33398	0.7165	0.6608	0.6694	0.6349	0.6571	0.6229
	±	±	±	±	±	±
	0.0085	0.0169	0.0103	0.0100	0.0031	0.0058

No significant differences were found between the rate of head growth in relation to body growth (regression coefficients, Table X). No sample exhibited a rate significantly different from unity, i.e., there was no real deviation from isometric growth.

To summarize, West Arm spawning males have longer heads than spawning males of other areas. There is a tendency for mature females of the North End to have shorter heads than those of the West Arm. The relation of head-length to body-length tends to be isometric in all areas. Mature males have larger heads than females in all areas.

REGRESSION OF PEDUNCLE-LENGTH ON FORK-LENGTH

No differences were found between sexes in peduncle-length. There were also no significant differences between areas in adjusted mean peduncle-length (Table XI). Over the range of sizes in the samples, the association of peduncle-length with fork-length was not strong. This is reflected in the reduction of the probability of regression in the North End sample to the 95% level. Thus, although the regression coefficients (Table XI) show great variation (and a progression, North End<West Arm<South End), only the extremes, North End and South End, are significantly different ($P<.01$). A regression coefficient of 1 in Table XI indicates isometry, and significant deviations from 1 indicate allometry.

TABLE XI. The relation of peduncle-length to body-length, 1951 kokanee.

Area	North End	West Arm	South End
Number of sample	52	52	52
Mean log. fork length	1.3367	1.3920	1.2733
Mean log. peduncle length	0.4678	0.4583	0.3736
Regression coefficient	0.391 ± 0.197	0.826 ± 0.297	1.420 ± 0.249
Prob. of regression = 0	. <0.05	<0.01	<0.01
Mean. log peduncle length at log. fork length of 1.33398	0.4668 ± 0.0035	0.4104 ± 0.0571	0.4598 ± 0.0198

In summary, there are no differences in mean peduncle length of kokanee from the three areas. There are also no differences between sexes. In the North End, larger kokanee tend to have disproportionately short peduncles. In the South End, larger kokanee tend to have disproportionately longer peduncles. In the West Arm, kokanee tend to have peduncles proportionate to size (isometry).

REGRESSION OF EYE-DIAMETER ON FORK-LENGTH

No differences in eye-diameter were found between sexes. The adjusted mean eye-diameter of West Arm kokanee (Table XII) was significantly greater than that of North End kokanee ($P<.01$) and that of South End kokanee ($P<.02$). Fish from the latter two areas had adjusted eye-diameters which were not significantly different.

Comparisons of regression coefficients (Table XII) indicated no significant difference between fish of any area in growth of eyes relative to size. The regression coefficient for all samples combined was 0.709.

In summary, West Arm kokanee had larger eyes than North End or South End kokanee. The relation of eye-diameter to size was similar in all areas.

TABLE XII. The relation of eye-diameter to fork-length, 1951 kokanee.

Area	South End	North End	West Arm
Number in sample	52	52	52
Mean log. fork-length	2.2733	2.3366	2.3920
Mean log. eye-diameter	0.9081	0.9388	0.9948
Regression coefficient	0.441 ± 0.140	0.828 ± 0.117	0.511 ± 0.168
Prob. of regression = 0	<0.01	<0.01	<0.01
Mean log. eye-diameter at log. fork length = 1.33398	0.9348 ± 0.0088	0.9366 ± 0.0021	0.9652 ± 0.0081

GROWTH RATES

Adequate samples of kokanee from each area were available only for mature fish and therefore growth rates could not be calculated directly from lengths. However, Mottley (1941) and Smith (1955) have shown that for rainbow trout scale size can be used directly as an index of growth. Milne (1948) has, in effect, demonstrated a similar relation for scales of sockeye salmon, and it has therefore been assumed that average scale size of kokanee gives an unbiased estimate of average fish length. Small differences between groups in mean scale row counts (127–130) were not enough to influence comparison of scale measurements.

The following scale measurements were made on scales of 26 kokanee of each sex from each area:

(a) Anterior radius to annulus I

(b) Anterior radius to annulus II

(c) Anterior radius between annulus I and annulus II

A preliminary analysis established no significant variation between sexes and therefore these were combined for comparisons between areas. The mean scale measurements are listed in Table XIII A and the probabilities of drawing any two of these means from a single population are listed in Table XIII B.

TABLE XIIIA. Mean scale measurements (in mm.), 1951 kokanee.

		West Arm	North End	South End	
a	Anterior radius to annulus I	1.5721	0.8631	0.8081	a
b	Anterior radius to annulus II	3.0412	2.3856	2.3092	b
c	Anterior radius from annulus I to annulus II	1.4691	1.5225	1.5011	c

TABLE XIIIB. Comparisons of scale measurements: the probability of drawing any two samples from the same population. a, b, and c refer to respective means of Table XIIIA.

	West Arm			North End		
	a	b	c	a	b	c
NORTH END						
a	<0.01	—	—	—	—	—
b	—	<0.01	—	—	—	—
c	—	—	>0.1	—	—	—
SOUTH END						
a	<0.01	—	—	>0.05	—	—
b	—	<0.01	—	—	>0.1	—
c	—	—	>0.1	—	—	>0.1

The outstanding feature of this analysis is the comparatively large size at the first annulus of scales from West Arm kokanee. They were 82% larger than North End scales and 88% larger than South End scales and these differences are significant ($P<.01$). Scale radius to the first annulus was greater in North End fish than in South End fish but the probability of this being due to chance was approximately 0.03.

Scale size of West Arm kokanee at the second annulus was correspondingly larger than those of North End or South End fish.

Mean scale radii from the first to the second annulus showed no significant differences between groups.

Assuming scale measurements to be estimates of relative fish lengths, then:

(a) The large size of kokanee in the West Arm is the result of a much greater rate of growth in the first year. In the second year, increments of growth are more nearly equal in all areas, and therefore the greater absolute size of West Arm fish is maintained.

(b) Growth rates of North End and South End kokanee in the second year are approximately equal, and are both greater than that of West Arm fish.

(c) Mature kokanee from the North End are larger than those of the South End chiefly as a result of maturing at four rather than three years of age.

Number of Eggs in Relation to Weight

Ten females from the West Arm, 26 from the South End and 23 from the North End were collected with intact ovarian membranes. From these fish the mean number of eggs per gram total body weight was calculated for each area. South End females averaged 3.44 ova per gram and this was significantly greater ($P<.01$) than either North End females at 2.33 ova per gram or West Arm females at 2.06 ova per gram. The latter two means did not differ significantly. Thus South End females produced a relatively large number of eggs for their size. (A more refined technique of comparison was not attempted because of the paucity of data.)

Spawning Period

Observations have not been sufficiently extensive to ascertain precisely the relative times of peak spawning or termination of spawning in various areas of Kootenay Lake. However, observations by the writer supported by those of fish cultural personnel of the British Columbia Game Commission indicate that kokanee in the South End commence spawning 10 to 15 days earlier than those of the North End. Commencement of spawning in the West Arm appears to be intermediate in time. Generally, the spawning period is September and October, and after the initial two weeks, kokanee are spawning in nearly all areas.

A summary, in general terms, of variation between areas is given in Table XIV.

The larger heads and eyes of West Arm kokanee probably result from greater development of breeding modifications which are also evident in the high degree of scale resorption, dermal thickening and breeding coloration.

TABLE XIV. Dissimilar characteristics of kokanee from three areas, 1951.

	West Arm	North End	South End
Predominant age at maturity	3	4	3
Size at maturity	large	intermediate	small
Growth rate in first year	high	low	very low
Vertebral count	intermediate	high	low
Scale row count	low	high	low
Gill raker count	high	high	low
Head length (males)	long	short	short
Growth form of caudal peduncle	isometric	negatively allometric	positively allometric
Eye diameter	large	small	small
Scale resorption and dermal thickening	extreme	moderate	slight
Spawning period (commencement)	intermediate	late	early
Ova per unit total weight of fish	low	low	high
Development of breeding coloration	high	intermediate	low

COMPARISON OF KOKANEE BETWEEN YEARS

THE SAMPLES

Subsequent to 1951, when seven streams in three areas were sampled, kokanee were collected from three areas in 1952, two areas in 1953 and three areas in 1954. Every sample was not examined with respect to all features studied in the 1951 samples but ages were determined, scale pattern observed, sizes recorded and vertebrae counted, except for the 1954 sample when age and scale pattern were not recorded. Samples were not taken from the same stream in each area in all cases. Thus in 1952 the South End sample was taken from Goat Creek and therefore to make comparisons more legitimate the Goat Creek sample is made representative of the South End in 1951. In 1954 the South End sample was taken from Sanka Creek, but reference to Tables VI and VIII will show that in 1951 there were no significant differences in size or number of vertebrae between Goat and Sanka Creek kokanee.

In the North End, Meadow Creek was sampled in years subsequent to 1951 and therefore the Meadow Creek samples were taken as representative of the North End for comparisons between years.

In the West Arm, Kokanee Creek was sampled in all years.

VARIATION IN AGE-CLASS DISTRIBUTION BETWEEN YEARS

Table XV shows that age-class distributions of spawning kokanee remain reasonably constant between years. The spawning component of each area is dominated by the same age-class each year. In the West Arm three-year-old fish contributed 87 to 96% to the spawning populations. Kokanee in the North End are almost 100% four-year-old fish at maturity. South End spawning kokanee consist of 87 to 97% three-year-old fish. Most of the deviations from the predominant year-class were young, precocious males common among Pacific salmon. Only in the South End (Goat Creek) were kokanee found which were older than the predominant year-class, and it will be shown below that these were strays from another area.

TABLE XV. Age class distribution between years.

Year	Age	West Arm		North End		South End	
		No.	%	No.	%	No.	%
1951	2	4	5	—	—	6	3
	3	70	95	—	—	155	88
	4	—	—	120	100	16	9
1952	2	—	—	—	—	2	2
	3	49	100	—	—	84	98
	4	—	—	73	100	—	—
1953	2	8	12	—	—	—	—
	3	57	88	1	1	—	—
	4	—	—	95	99	—	—

VARIATION IN SIZE BETWEEN YEARS

Table XVI shows the variation in mean fork-length between years. As no significant difference was found between sexes, they were combined to form larger samples in all cases. Although the size of kokanee varies considerably from year to year, the progression West Arm > North End > South End is stable and the difference between their means significant ($P<.01$) throughout four years of sampling. Variation between years tends to be in the same direction in all areas.

TABLE XVI. Variation in mean fork-length between years, in centimetres.

	1951	1952	1953	1954
West Arm	24.66	22.62	23.28	23.62
North End	21.40	19.95	20.49	22.03
South End	18.19	15.62	—	18.51

VARIATION IN VERTEBRAL COUNT BETWEEN YEARS

Distributions of vertebral counts are shown in Table XVII. It has been noted previously that the number of vertebrae did not vary significantly between streams in the same area in 1951. Comparisons between years indicated significant and sometimes parallel variation in all areas. However, differences between areas were significant ($P<.01$) each year and the progression North End > West Arm > South End remained unchanged during the four years.

VARIATION IN SCALE CHARACTERISTICS AND SCALE RESORPTION

Scale characteristics were not compared quantitatively between years but scales of the 1951, 1952 and 1953 samples were examined for age determination. The comparatively large radius to the first annulus of West Arm kokanee was maintained as a striking characteristic throughout the three years. Scale patterns of North End and South End kokanee also appeared to remain stable.

West Arm kokanee continued to display extreme scale resorption and dermal thickening as well as a high development of breeding coloration in comparison with fish from other areas.

TABLE XVII. Distributions of vertebral counts in three areas of Kootenay Lake, 1951 to 1954.

Area and year	Number of vertebrae									Mean
	60	61	62	63	64	65	66	67	68	
NORTH END										
1951	—	—	—	—	—	20	24	8	—	65.77
1952	—	—	—	—	—	11	23	15	3	66.19
1953	—	—	—	—	10	25	11	6	—	65.25
1954	—	—	—	1	6	8	9	—	—	65.04
WEST ARM										
1951	—	—	—	2	16	20	14	—	—	64.90
1952	—	—	—	4	12	15	7	—	—	64.66
1953	—	—	—	4	20	19	7	2	—	64.67
1954	—	—	1	6	12	9	1	—	—	64.10
SOUTH END										
1951	—	—	—	10	14	24	4	—	—	64.42
1952	—	—	2	8	26	15	1	—	—	64.09
1954	1	1	3	5	5	1	—	—	—	62.94

SUMMARY OF COMPARISONS BETWEEN YEARS

Examination of age and size at maturity, vertebral count, scale pattern and scale resorption in samples from three areas over four years indicates that, while significant variation of some characters occurred between years, the differences between kokanee from each of the three designated areas were stable throughout this period.

DEGREE OF STRAYING BETWEEN HOME STREAMS

By examination of scale pattern, size, scale resorption and in one case, vertebrae and scale rows, it was possible to identify kokanee spawning in an area other than their native or home area. The number and proportion of these strays are shown in Table XVIII.

TABLE XVIII. The number and origin of spawning kokanee identified as strays from their home area.

Area and year	Stream	Total No. in sample	Strays		Origin of strays
			No.	%	
1951					
West Arm	Kokanee Cr.	74	3	4.0	South End
	Redfish Cr.	97	8	8.2	South End
North End	Lardeau R.	102	0	0	
	Meadow Cr.	120	0	0	
South End	Cultus Cr.	114	0	0	
	Sanka Cr.	78	1	1.3	West Arm
	Goat Cr.	177	16	9.0	North End
1952					
West Arm	Kokanee Cr.	49	2	4.1	South End
North End	Meadow Cr.	73	0	0	
South End	Goat Cr.	86	0	0	
1953					
West Arm	Kokanee Cr.	65	2	3.1	South End
North End	Meadow Cr.	96	0	0	
	Totals	1131	32	2.83	

Of 1,131 kokanee sampled over a three-year period, a total of 32 or 2.8% were identified as strays (21 males, 11 females). Of this number, 15 were South End fish which were spawning in the West Arm, one was a West Arm fish spawning in the South End, while no strays from other areas were found among the 391 kokanee examined from the North End. The largest group of strays was found in Goat Creek in 1951 (South End). This group of 16 fish comprised 9% of the collection from this stream and was sufficiently large to form a sample for statistical comparisons. Mean fork-length, vertebral count, scale row count and scale radii did not differ significantly from North End kokanee and, except for scale radii, did differ significantly from South End kokanee. Thus this group could be designated with some confidence as strays to the South End from the North End.

Because morphological variation between streams was slight, and significant only in the case of size, it was impossible to evaluate straying within areas. This homogeneity within areas suggests that considerable straying occurs between adjacent streams in each area.

THE TRANSMISSION OF RACIAL CHARACTERISTICS TO OFFSPRING

Three groups of kokanee were reared experimentally to measure the effect of environment on size and number of vertebrae. North End parent stock were collected in Meadow Creek, West Arm from Kokanee Creek and South End from Sanka Creek. These collections were transported separately, alive, by tank truck to a hatchery at Nelson and held until mature in separate concrete ponds provided with flowing water and gravel bottoms. No loss of fish occurred in these operations. All three lots were artificially spawned on September 28. Because of differences between parental lots in time of maturation it was not possible to utilize all fish collected. However, milt and eggs from all fish of each lot gravid at the time of spawning were combined, regardless of the resultant sex ratio, to provide a maximum of parental variability. Fertilized eggs were placed in three parallel hatchery troughs supplied with water from a common source. After hatching, the young fish were fed until a size convenient for enumeration of vertebrae had been attained (3–5 cm.).

Number of Vertebrae

The distributions and means of vertebral counts of parent kokanee and progeny can be compared in Table XIX. As the parent sample from each area was restricted to those individuals which matured concurrently and were artificially propagated, some of the parental samples are small but no extreme departures from normality are evident. As noted previously, the mean number of vertebrae of parent kokanee differed significantly between areas ($P<.01$) and formed a progression North End > West Arm > South End. Similarly, mean number of vertebrae of progeny differed significantly between areas ($P<.01$) and formed a progression North End > West Arm > South End. Thus progeny grown in identical environments preserved differences which had been observed to be stable over four years in native kokanee from three areas in Kootenay Lake. Difference between means was reduced in offspring, being a maximum of 2.10 vertebrae in parents and 1.19 in progeny.

TABLE XIX. Distributions of vertebral counts of parent kokanee (P) and progeny (F), 1954–1955.

Area		Number of vertebrae 60	61	62	63	64	65	66	67	Mean
North End	P	—	—	—	1	6	8	9	—	65.04
	F	—	—	—	1	11	29	9	2	65.00
West End	P	—	—	1	6	12	9	1	—	64.10
	F	—	—	1	7	23	18	3	—	64.29
South End	P	1	1	3	5	5	1	—	—	62.94
	F	—	1	4	15	18	12	2	—	63.81

The possibility was considered that egg size might be related to the number of vertebrae since it may well govern to some extent the number of somites differentiated in the embryo. Unfortunately, egg sizes were not determined but samples taken two weeks after hatching would accurately reflect egg size since feeding had barely begun. Twenty-six specimens were chosen at random from large samples taken two weeks after hatching. Mean fork-length of South End progeny (2.14 cm.) was significantly smaller ($P<.01$) than North End progeny (2.24 cm.) or West Arm progeny (2.26 cm.). The difference in size between the latter two samples was not significant. Thus, although South End kokanee which develop from small eggs have the lowest number of vertebrae, differences in vertebrae counts of North End and West Arm fish were unrelated to egg size.

FORK LENGTH

Differences between areas in fork length of parent kokanee in 1954 have been noted previously. These differences were significant and formed a progression West Arm > North End > South End identical with that of samples from previous years.

Progeny of South End kokanee at six months had a mean fork length of 3.66 cm. which was significantly smaller ($P<.01$) than North End (4.11 cm.) or West Arm kokanee (4.13 cm.). However, North End and West Arm progeny did not differ significantly in fork length. Examination and measurement of scales from wild stock in previous years had shown a strikingly high first year growth rate for West Arm kokanee, while differences between North and South End were small. Thus, not all of the differences in first year growth characteristics of wild parents were evident in progeny grown under uniform environmental conditions. Differences similar to those of parents might have developed if progeny had been raised for a full year. However, differences between groups in their responses to a *hatchery* environment may confound an experiment on growth rates.

DISCUSSION

SOME EFFECTS OF ENVIRONMENT ON ANATOMICAL CHARACTERS

Much of the observed morphological variation between groups of kokanee in Kootenay Lake probably reflects environmental differences. Precise data on local environmental variation are not available, but some physical features of the lake suggest that environmental conditions may differ greatly between major areas.

The North End is dominated by the large inflow of Lardeau River. During the summer this river is colder than the surface water of the lake and, on entering, goes beneath the surface to a depth of equal density (temperature) and flows southward along the westward lake margin for a considerable distance (Larkin, 1951). In the process of mixing, heat is added to the deeper lake strata.

The South End is dominated by the inflow of Kootenay River which, being warmer than the lake water, spreads out over the surface. The mineral content of Kootenay River is much higher than that of Lardeau River and this has a fertilizing effect on the South End which is reflected in a higher production of bottom organisms (Larkin, 1950).

The West Arm is comparatively narrow and, since it drains the entire inflow to the lake, it has a perceptible current throughout its length. Because of a shallow sill at the entrance, water is drawn from surface strata of the main body of the lake. During the growing season these surface strata should supply relatively warm water to all levels of the West Arm. Plankton produced in the main body of the lake will be drawn into the West Arm by this flow of surface water. These features probably have a profound effect on abundance of food for kokanee.

Geographical variation in growth rates of kokanee probably reflect variation in availability of food as the result of differences in limnological conditions. Since kokanee migrate to the lake before feeding, stream conditions could affect growth rates only through the modifying influence of temperature on the length of the incubation period and therefore the time at which feeding begins. Breeding experiments suggest that differences in growth rates during the first year of life are probably due to phenotypic variation. A gradual random dispersion after entering the lake from the spawning streams would insure that kokanee were most subject to the modifying influence of local limnological conditions during their first year. With increasing size and mobility, temporary or permanent penetration of other lake areas would tend to reduce racial growth rate differences in older age classes.

The racial differences found in head-length and eye-diameter may be largely due to differences in the development of breeding modifications. However, these racial characteristics as well as differences in the growth form of caudal peduncles could be influenced by the variability of growth rates. Martin (1949) has shown that rate of early development and subsequent rate of growth may both influence body form through their effects on body size at inflections between growth stanzas.

The influence of environment on the development of secondary sex characters such as scale resorption, dermal thickening and development of breeding color is unknown, but appears to be associated with size at maturity in kokanee of Kootenay Lake. Ricker (1938) found a difference in degree of scale resorption between two populations of non-migratory sockeye in Cultus Lake. Although Ricker (1940) ascribed a genetic basis to this difference in scale resorption, it was in this case also partly associated with size at maturity.

Svärdson (1950) suggests that growth rates of fishes are related to age at sexual maturity. A rich food supply may cause accelerated physiological aging and an early sexual maturity. On the other hand, very poor food supply may also produce forms maturing early in spite of retarded physiological aging. Selection under these extremely poor conditions may favour animals possessing hormonal mechanisms permitting early sexual maturity. While there is no experimental evidence for the operation of these mechanisms in Kootenay Lake kokanee, it can be noted that the two populations having the largest and smallest mean size mature a year earlier than the population having an intermediate mean size.

Many environmental factors have been shown to influence the number of meristic parts in fishes. Schmidt (1918) showed that temperature and salinity could affect the number of meristic parts, and Hubbs (1926) discussed the effects of developmental rate. Rounsefell and Dahlgren (1932), Runnstrøm (1933), and Tester (1938) correlated differences in vertebral counts of herring with environmental temperature during early development. Tåning (1944, 1952) and Lindsey (1954) showed by carefully controlled experiments that some meristic counts could be raised by either high or low temperature during early development of embryos.

Neave (1936) has shown that the number of lateral line scales of *Salmo* is only partially dependent on the number of somites. Mottley (1934) was able experimentally to decrease lateral line scales by increasing temperature. Scale row counts of Kootenay Lake kokanee are not completely correlated with number of vertebrae and to this extent have probably been influenced independently by environmental factors.

While racial differences in vertebral count of kokanee in Kootenay Lake have been shown to be remarkably stable both in wild populations and in those grown in similar environments, changes due probably to environmental influences have occurred. The parallel reduction in vertebra count in all areas in 1954 suggests that common environmental factors were affecting all three populations. Mean vertebral counts have changed significantly within races between years, between wild parents and offspring sampled three years later, and between wild parents and offspring of one group (South End) raised in a hatchery. Racial differences in mean vertebral counts were somewhat reduced when progeny were raised in a uniform environment.

Isolating Mechanisms

The pronounced tendency of Pacific salmon to return to and spawn in the stream of their natal origin has been well documented. Walford (1939) after an extensive survey of literature, concluded that, on the basis of scale marks, stocking experiments, cyclical abundance, and marking experiments each river and even each tributary may have its own local self-perpetuating stock of Pacific salmon. In Kootenay Lake, the homogeneity of kokanee populations on their spawning areas indicates a pronounced tendency to "home" to parent streams. This homing behaviour of kokanee is considered to be of prime importance in the isolation of races within the lake.

The intense segregation of racial stocks during reproduction may not be completely overcome during growth and maturation of the ensuing generation. Differences in growth rate suggest strongly that kokanee tend to remain within their home area at least during the first year of life, and it is possible that complete randomization throughout the lake never occurs. Convergence of racial growth characteristics in older groups may be due to some quality of food such that it is not equally available in all areas to underyearling fish, but is equally available in all areas to older fish. Since kokanee are largely plankton feeders their movements in search of food would tend to be random but the large areas involved in Kootenay Lake may preclude their random distribution throughout the entire lake during their short lives of 2½ or 3½ years.

Svärdson (1950) believes that schooling behaviour is important in maintaining the separate identity of sympatric species of coregonids. Smith (1957) found that two groups of rainbow trout with similar parental background but different environments during early life, tended to maintain separate aggregates 1½ years after transfer to a small lake. The strong schooling behaviour of young sockeye is well known (Hoar, 1954). The behaviour of kokanee in lakes has not been studied but observations suggest that schooling is common and if so, this may aid in maintaining separation of racial stocks in Kootenay Lake.

Significance of Genotypic Divergence

While a genetic basis is unlikely for most of the racial characteristics of kokanee in Kootenay Lake, strong homing tendencies, perhaps augmented by other isolating mechanisms, lead to intense segregation during reproduction and have resulted in some genetic divergence. Few isolating mechanisms are complete. Even the most geographically isolated populations may be visited by strays from nearby populations. The divergence of two populations merely indicates that the combined effects of mutation, selection and random fixation outweigh the equalizing tendencies of gene flow. A balance between these various forces may be reached at some point before divergence has reached the species level. This state of equilibrium has probably been attained in the groups of kokanee in Kootenay Lake. Since some three per cent of mature fish interbreed with groups other than their own, genetic differences are unlikely to increase toward speciation. While it is unlikely that differences in number of vertebrae are of adaptive significance, they may be associated with anatomical or physiological variations which have survival value.

It is highly probable that similar genetic divergence has occurred between groups of sockeye. The general lack of success of large scale rehabilitation programs in which salmon were transplanted to new areas within the same river system (Foerster, 1946) suggests some measure of adaptive genotypic divergence. Morphological variability between sockeye races has been observed (Hamilton, 1947; Broadhead, 1949). While experimental work designed to demonstrate genetic differences would be desirable, it appears reasonable to believe that these differences do exist and to predicate management on that assumption.

SUMMARY AND CONCLUSIONS

1. Kokanee (*Oncorhynchus nerka*) were collected from spawning runs to seven streams tributary to Kootenay Lake, British Columbia.

2. Preliminary examination of morphometric features of these kokanee indicated that in Kootenay Lake they were separable into three groups:

(a) South End fish, averaging approximately 18.5 cm. and 55 gm. and spawning at 3 years.

(b) North End fish, averaging approximately 21.5 cm. and 105 gm. and spawning at 4 years.

(c) West Arm fish averaging approximately 24.5 cm. and 155 gm. and spawning at 3 years.

3. Further examination disclosed that, within each area, kokanee were similar in growth rate, vertebral count and development of secondary sex characters.

4. Samples from a representative stream of each area were found to differ in age at maturity, size, growth rate in the first year, vertebral count, scale row count, gill raker count, head length of males, growth form of caudal peduncle, eye diameter, development of secondary sex characters, ova per unit total weight and commencement of spawning period.

5. Examination of age, size, vertebral count, scale chracteristics and scale resorption in samples from three areas over a period of four years indicated that while significant variation occurred between years in some cases, this variation did not obscure the significance of variation between areas in any one year. Differences between areas remained stable over four years.

6. By examination of scale characteristics, size, scale resorption, vertebrae and scale rows, it was possible to identify kokanee spawning in an area other than their home area. Less than three per cent of 1,131 specimens examined had strayed from the area of their natal origin.

7. Progeny of kokanee from three areas were propagated artificially in identical environments from fertilization to six months after hatching. Characteristic parental differences in number of vertebrae were transmitted to offspring. Differences in growth rate were not transmitted.

8. Some effects of environment on anatomical features are discussed and it is concluded that many of the racial characteristics of kokanee in Kootenay Lake may be due to phenotypic variation.

9. It is concluded that the strong tendency of kokanee to spawn in the stream of their natal origin is the principal factor isolating three essentially discrete kokanee races in Kootenay Lake, and has led to some genotypic divergence, despite an average interbreeding of three per cent.

ACKNOWLEDGMENTS

The author wishes to express particular appreciation of the advice and support of Dr. P. A. Larkin both as Chief Fisheries Biologist for the British Columbia Game Commission and in his present position as Director of the

Institute of Fisheries, University of British Columbia. The greater part of the work was done under his direction in partial fulfilment of the requirements for the degree of Master of Arts in the Department of Zoology at the University of British Columbia. Dr. W. A. Clemens also gave advice during this phase of the work.

Dr. C. C. Lindsey kindly gave critical advice and suggestions during preparation of the manuscript. Dr. D. P. Scott gave advice on statistical procedures.

Much of the project was financially supported by the British Columbia Game Commission and the following personnel gave assistance in field collections and artificial propagation: R. A. Rutherglen, R. A. McRae, E. Hunter and H. Sparrow.

G. F. Hartman and D. E. McAllister kindly assisted in clearing and staining specimens.

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Evolution and Distribution of the Coregonids[1]

By Stanford H. Smith
United States Fish and Wildlife Service,
Ann Arbor, Michigan

ABSTRACT

Increased knowledge of the morphological and physiological plasticity of the coregonids has minimized the significance of conflicting morphological data that have retarded the development of an evolutionary theory. Of the four phyletic lines recognized through world-wide studies, *Coregonus* originated in the lake and stream area of northwest Eurasia, *Stenodus* and *Prosopium* evolved in the rivers of Siberia and northwest America respectively, and *Leucichthys* became differentiated in the lake-studded area of northeast America. Isolation and range extension were facilitated by events of the Pleistocene epoch. Inter-continental exchange most likely took place in the Bering Strait region. Representatives of each group in its area of origin are highly variable. Range extensions of each group are characterized by lesser morphological variability and at the extremes only one or two relatively stable species remain.

For many decades the complex nature of the coregonids has confounded taxonomists who have sought an adequate system of describing them. The frustrated efforts of early workers caused many of them to feel that conventional taxonomic procedures were inadequate for the description of this group. In recent years the investigators of the coregonids have not depended so strongly on classical morphometry but have placed greater emphasis on sound reasoning and experimentation.

The coregonids are characterized by a high degree of environmentally controlled morphological (Hile, 1937) and physiological (Frey, 1955) plasticity and, due to their recent origin in geologic time, resemblance is close among forms of the different phyletic lines. Svärdson (1945, 1949–1953), through chromosome studies and transplantation experiments, has demonstrated some of the genetic and environmental bases that underlie the high degree of plasticity. This positive evidence of the high degree of variability that exists among the coregonids reduces the significance of much of the conflicting morphological data that have long retarded the development of an overall theory of coregonid evolution, making the present discussion possible.

The first descriptive work on coregonids was done in Europe where the single genus *Coregonus* was established to include all known coregonids of that area. As knowledge was subsequently gained of the coregonids throughout their circumpolar range, four general groups were recognized and have been described as genera: *Coregonus*, (*Artedi*) Linneaus (1738); *Stenodus*, Richardson (1836); *Leucichthys*, Dybowski (1874); and *Prosopium*, Milner (1878). The four genera have long been used to depict the natural phyletic lines of the coregonid complex.

[1]Received for publication March 6, 1957.

J. Fish. Res. Bd. Canada, 14(4), pp. 599–604, 1957.
Printed in Canada.

In Europe, however, where nearly all coregonids belong to the genus *Coregonus* (*sensu stricto*), a single genus is still used for all forms except *Stenodus*. Some workers in other areas have combined two or more of the genera for various reasons so that the problem of the generic standing of the four basic coregonid groups is still under debate.

The problem of generic standing is not, however, germane to the present discussion which is concerned only with origins, evolutionary development, and distribution. A review of the complicated controversial, and often confusing literature on coregonid taxonomy is, therefore, unnecessary. The reality of the four basic groups is, nevertheless, undeniable and I shall accordingly for convenience, apply to them the generic names that have been commonly accepted by investigators in North America.

The range of each coregonid genus has a "nucleus area" where the representatives occur in a wider variety of environments and forms, and where they show a higher degree of plasticity than elsewhere. For *Coregonus* this area is northwest Eurasia, for *Prosopium* northwest America, and for *Leucichthys* northeast America. Although *Stenodus* has been less completely studied, it appears that the "nucleus area" where it occurs in greatest diversity must be in Siberia (Dymond and Vladykov, 1934). The environmental preference (lake or stream) of each genus over its entire range tends to match the predominant environment where it is represented in its greatest variety of forms. This relationship strongly suggests that the "nucleus areas" are the localities in which the several genera differentiated from a common progenitor.

The *Coregonus* group which originated in northwest Eurasia, an area with an abundance of suitable lakes and many cold streams, is found throughout its range mostly in lakes, but occurs also in many streams particularly in the cooler northern regions. *Stenodus* and *Prosopium* differentiated in Siberia and northwest America, respectively, where rivers predominate; both are thought of as river forms because of their preference for rivers elsewhere in their ranges, although they also occupy some lakes. The *Leucichthys* group that originated in the flat, lake-studded area of northeast America shows a strong preference for lake habitats over its entire range. This similarity between the habitat preference of each group and the predominant environment of its area of origin suggests that primary divergence of the groups may have been a process of adaption to different environments.

The northern, circumpolar distribution of the cold-stenothermic coregonids closely follows the limits of the area strongly influenced by cooling climate and glacial ice during the Pleistocene epoch. Changes in the quantity and temperature of water and the advance and recession of ice sheets during the Pleistocene must have had a tremendous effect on the distribution of coregonid fishes.

It is possible that the progenitor of coregonids was not unlike *Stenodus*, which bears a closer resemblance to the salmonids than do other coregonids because its teeth are least reduced in size and its members have an inclination to undergo extensive migrations. The migratory tendency of a *Stenodus*-like progenitor, with a preference for extreme northern environments characteristic of the present-day *Stenodus*, could have resulted in a circumpolar distribution of this

form prior to the Pleistocene. This ancestral form must have been a well-defined yet plastic member of the fish fauna of that time, particularly in its habitat preference. During the first glacial period (Nebraskan-Günz) the extension of cold-water environment and the forced evacuation of certain areas caused by the encroachment of ice sheets brought about a southerly extension of the range of this form. During the subsequent interglacial time (called Aftonian in North America), it would have survived in many southern environments where populations developed to fit the general conditions of the different segments of its range. Thus lake forms evolved in the lake region of northeast America, river forms in northwest America and Siberia, and lake and stream forms in northeast Eurasia. These four regions are the "nucleus areas" of the present genera. During the estimated 200,000 years of the warm Aftonian interglacial period basic differences developed among the representatives of the four areas. The divergence must have been primarily physiological as morphological differences among the basic groups are limited even today. Although the divergent characteristics that separated the four groups may have been small—even superficially insignificant—they were great enough for the groups to maintain their identities in spite of mixing that took place during later glacial and interglacial periods. With such persistent separation there is little probability that these phyletic lines will ever coalesce.

The present distribution of each of the four genera that differentiated early in the Pleistocene must have come about as the result of processes related with subsequent glaciation. The onset of a glacial period with its increased precipitation and cooling climate would extend suitable coregonid habitat. The advance of the several ice sheets would force movements into new waters and cause a mixing of the fish from different areas. As the sheets later receded the coregonids followed, again bringing adjacent groups together. This process repeated during succeeding glacial periods could have been an important agent in extending the ranges of the four groups to approximate the present distribution.

Although this discussion of the evolution and distribution of the coregonid genera has been given in terms of the entire Pleistocene, it is not inconceivable that the process might have been completed in a shorter time. Certainly, if the coregonids always had the high degree of plasticity that they now exhibit, differentiation could have taken place more recently. The exact timing of these geological and biological events is not, however, of immediate importance. Of much greater significance is a reasonable description of the sequence of occurrences that must have taken place to bring about the present coregonid complex. This description, if properly framed, can serve as a basis for understanding and adequately describing present-day forms.

The paths of movement that were probably followed by the four basic groups in attaining their present distribution are illustrated schematically in Fig. 1. The Bering Strait region appears to be the most likely site for an exchange between continents. Although the Bering Strait may have sometimes been a salt-water barrier, it was non-existent at times during the Pleistocene. Furthermore, coregonids of all four genera occur in brackish water in that region (Walters, 1955) and some forms can tolerate high salinities. Thus the transfer of coregonids between Asia and North America presents no problem.

The assumptions as to avenues of dispersal (Fig. 1) are substantiated by the characteristics of each genus over its range. *Leucichthys*, for instance, is represented by a variety of highly plastic species in northeast America where it originated. Moving westward from this area, the variety and plasticity of forms in this group decreases and at the extreme end of its range in northwest Europe it is represented by the relatively stable *Coregonus* [*Leucichthys*] *albula*. Although the Europeans include this form in the genus *Coregonus* (subgenus *Argyrosomus*) because of its morphometric similarities with some other members of the restricted genus *Coregonus*, contacts with coregonid workers in Europe revealed that the general features (sight recognition) so clearly separate *C. albula* from other local *Coregonus* that it is not considered in discussions of systematic problems of the European coregonids. Investigators in Europe and North America have recognized *C. albula* to be closely similar to the lake herring or cisco (*L. artedi*) of North America. Unquestionably both are representatives of the same phyletic line. The progenitor of the many *Leucichthys* forms that now have a nearly circumpolar distribution most likely resembled the lake herring. The lake herring lives in the widest variety of habitats in the "nucleus area" of its genus. Such an adaptable form would be best suited to survive in the varied environments encountered in range extension. Also, most members of the *Leucichthys* group found outside of the Great Lakes area, where the widest variety of forms are found, resemble *artedi* more closely than any other species within the area.

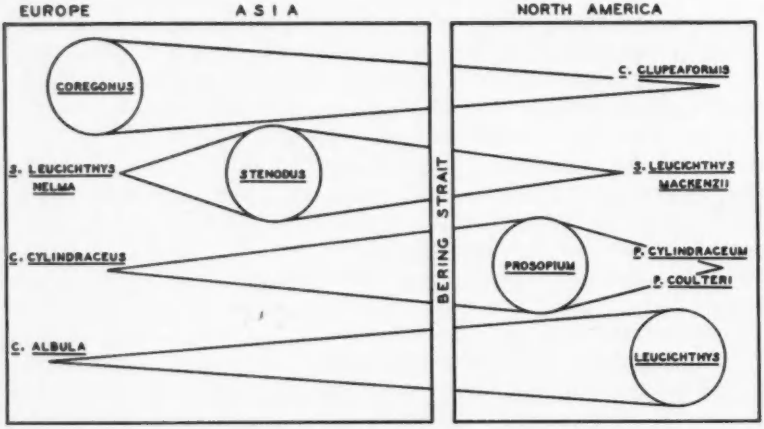

FIG. 1. Schematic diagram of the development areas and dispersal routes of coregonid genera.

The distribution of the *Coregonus* group follows the pattern of *Leucichthys* but in reverse (west-east) direction. From a center in north and central Europe where varied and highly plastic forms are found the variety and plasticity decrease in the easterly extension of the range. At the extreme eastern limit this

genus is represented by one relatively stable species, *C. clupeaformis*. The form that contributed most to present-day species of *Coregonus* may have resembled *C. lavaretus* as this fish seems to be highly adaptive and is similar to most members of its group outside Europe. The designation of a form most likely to fill this position would, however, be best suggested by someone who has worked extensively with coregonids in Europe and Asia.

The *Prosopium* group has extended its range to both the east and the west. From a center in the western mountains of North America the variety of forms diminishes in each direction. The genus is represented by two relatively stable species (*P. cylindraceum* and *P. coulteri*) in the eastern extremity of its range in northeast America and by one species (*C.* [*Prosopium*] *cylindraceus*) at the western extremity in northern Russia. *P. cylindraceum*, the most adaptive species of this group, probably resembles the common ancestral form.

The lack of adequate information about *Stenodus* from what must be its "nucleus area" in Siberia makes generalization difficult. *Stenodus* appears, however, to be more stable than other coregonid groups although further study may show that the characteristics of variability in different parts of its range resemble those of the other genera.

These views on the evolution and distribution of the four phyletic lines of coregonids have been described in a greatly simplified form. From a morphological standpoint a number of irregularities may exist among the several genera. These are to be expected in a group with the morphological and physiological plasticity of the coregonids. During the process of range extension, members of each phyletic line were undoubtedly subjected to environmental pressures that may have promoted ambient morphological developments in local populations. Isolated populations of one genus may have, through retrogressive or parallel development, acquired one or more characteristics common to most members of another genus. Despite this "concealing" type of development, experienced investigators have been able to recognize through other characteristics the true group to which the aberrant population belongs. Inconsistencies of this type do not, therefore, detract seriously from the validity of the ideas expressed here.

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Fresh Water Transport Determination from the Heat Budget with Applications to British Columbia Inlets[1]

By G. L. Pickard and R. W. Trites[2]
Institute of Oceanography
University of British Columbia, Vancouver, B.C.

ABSTRACT

Fresh water entering British Columbia inlets moves seaward, mixing with and entraining salt water from below. A new method, based on a heat budget analysis, is developed to determine the mean seaward movement of the brackish layer. The method is also applied to gain information on the mixing process and to determine the depth from which salt water is entrained into the surface layer.

The values of mean transport calculated in this way are found to be in good agreement with those derived from other methods. The method offers some distinct advantages over direct methods for determining fresh water inflow and circulation, since results can be obtained quickly, with little effort, and without the necessity for anchoring a ship.

INTRODUCTION

During the past few years an oceanographic study of British Columbia mainland inlets has been undertaken (Pickard, 1955). Preliminary surveys were designed to furnish a general knowledge and classification of the inlets, before a more intensive and detailed study of specific features was initiated.

The British Columbia inlets are elongated indentations of the coastline varying in length from 5 to 90 miles and in width from ½ to 3 miles (Fig. 1). They are relatively deep with steep-sided basins. Depths are usually less near the mouth than in the body of the inlet, although the sill is not shallow enough to cause stagnation. The average mid-channel depth of the inlets is approximately 330 metres, but 550 metres is common, and the greatest depth recorded is 732 metres (Jervis Inlet). The sides of the inlets above the water surface are mostly steep and rugged, slopes of 45° or more being not uncommon.

Because of the free connection with the sea, the bulk of the water in the inlets is saline. All of the inlets receive fresh water drainage which exceeds evaporation and consequently there is a net seaward movement of water. The fresh water entering the inlets overrides the heavier salt water, but, as it proceeds seaward, it mixes with and entrains salt water from below. A schematic diagram of the structure and circulation in the inlets during the summer months is shown in Fig. 2.

During the summer the surface water at the inlet head is substantially fresh (salinity less than 1‰), forming a layer 2 to 9 metres in depth, depending on the inlet and the stage of the runoff. At 4 to 12 metres the salinity increases to 25‰ or more and at 18 to 20 metres it has increased to more than 0.9 of its value at

[1]Received for publication December 21, 1956.

[2]Present address: Fisheries Research Board of Canada, Atlantic Oceanographic Group, St. Andrews, N.B.

J. Fish. Res. Bd. Canada, 14(4), pp. 605–616, 1957.
Printed in Canada.

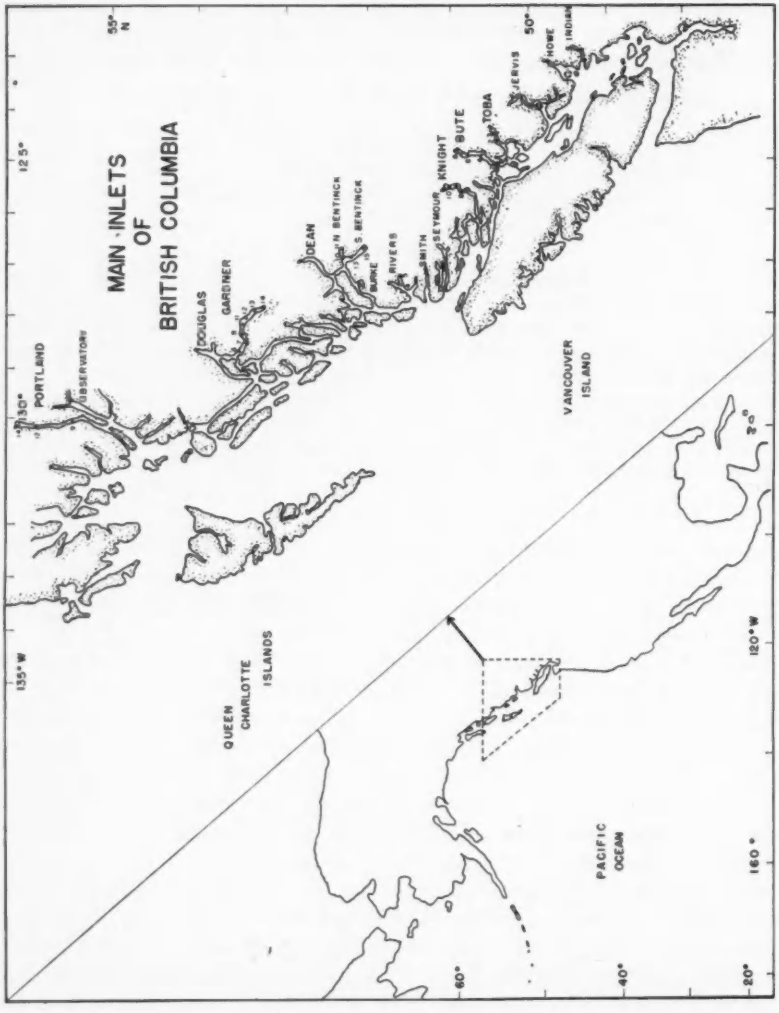

Fig. 1. Inlets of the British Columbia mainland coast.

the deepest point (referred to as the base salinity). The salinity in the top layer increases down the inlet reaching values near the mouth of 0.7 to 0.9 of the base salinity. These values correspond approximately to the surface salinities of the surrounding coastal waters. Thus at the head of the inlet the distribution approximates a two-layer system with a very sharp transition zone (halocline). Towards the mouth the halocline is less apparent and may even be non-existent, so that on the basis of salinity no distinct layers can be identified.

During the summer months the surface water is usually the warmest part of the column. The brackish surface layer is nearly isothermal. A rapid decrease in

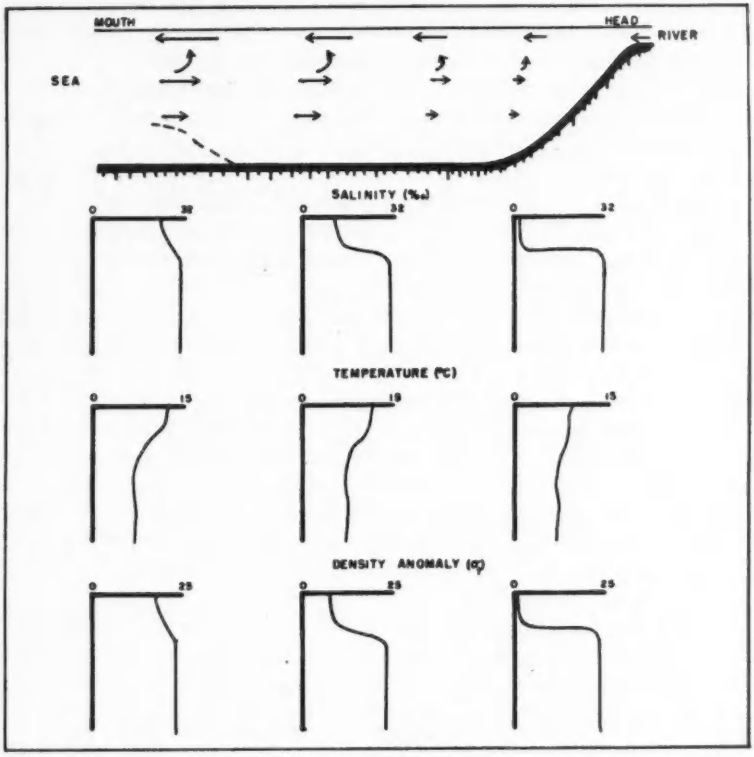

FIG. 2. Schematic diagram of circulation, and salinity, temperature and density anomaly structure of British Columbia inlets.

temperature (thermocline) occurs below this, followed by a fairly steady decrease until a minimum is reached at 60 to 90 metres depth. The temperature of the deep bottom water remains constant throughout the year at approximately 8° C. in the southern inlets and 6° C. in the northern ones. A critical feature, and the one upon which the present study is based, is that in summer the temperature in the top layer usually increases from head to mouth, the increase ranging from less than 0.5 degree (C.) to as much as 5 degrees. This increase in temperature is the result of absorption of heat from sun and atmosphere. In winter months the temperature usually decreases toward the mouth, which is indicative of a net loss of heat to the atmosphere.

Typical density curves for an inlet are shown at the bottom of Fig. 2. The shape of the curves is very similar to the salinity curves, indicating that, in contrast to most open ocean areas, temperature plays only a minor role in determining the density distribution in the inlets. Consequently, during most seasons of the year the density may be considered to a good degree of approximation to be directly proportional to the salinity.

Observations indicate that the thickness of the brackish layer does not increase down-inlet, so that the bulk of the fresh water remains near the surface. Since this layer becomes more saline to seaward, the velocities within it must increase seaward. If the quantity of salt in the inlet is to remain constant, then there must be a corresponding up-inlet flow at deeper levels to balance the net outflow of salt in the surface layer.

There have been a number of theoretical studies of estuaries during recent years (e.g. Cameron, 1951; Stommel and Farmer, 1952; Pritchard, 1952) that have been valuable in shedding light on the nature of the circulation, the mixing process, the distribution of properties, and the factors which may control or relate to them. Among the parameters which need to be known if the results are to have practical value are the volumes of fresh water being discharged into the estuary, and the velocities at different positions along the estuary. Because the area is sparsely populated, only a few of the numerous rivers draining into the British Columbia inlets are, or ever have been, metered. Also, precipitation measurements are only available for widely separated localities. Consequently, direct quantitative data on runoff are very limited. Likewise, very few direct current measurements have been made in the inlets. Those available were obtained only after considerable effort, since the anchoring of a ship in such deep water and keeping it stationary is a major problem in itself. Moreover, a large number of measurements are required before a reliable average value can be determined. Therefore, any method which yields information on the runoff, currents, and volume transports, even if only mean values, is valuable. It was for this reason that an examination was made of the possibility of determining the volume transport by studying the heat budget in the inlets.

HEAT BUDGET METHOD

In the analysis presented here, three conservation principles are involved, those of heat, of volume, and of salt. The complete equation expressing a heat balance in any part of the sea is given (Sverdrup *et al.*, 1942) by:

$$Q_s - Q_b - Q_e - Q_h - Q_\theta + Q_v \equiv 0 \qquad (1)$$

where

Q_s = heat received by insolation,
Q_b = back radiation from the sea surface,
Q_e = heat required for evaporation,
Q_h = conduction of sensible heat to atmosphere,
Q_θ = heat required locally to change the temperature of the water,
Q_v = heat brought into the region by currents or processes of mixing.

The first four quantities in equation (1) can be estimated from meteorological observations, and the fifth (Q_θ) measured directly. Consequently Q_v can be determined from equation (1). The application of the equations of continuity of volume and salt then permits the mean transport to be determined.

In order to apply equation (1) the following observations are required: air temperature, relative humidity, wind-speed, cloud cover, and the vertical temperature profile in the sea. In addition it is necessary to know the daily totals

of solar radiation (direct and diffuse) received at the sea surface in the absence of clouds.

Using the equations given by Sverdrup *et al.* (1942, Chap. IV), the quantities Q_b, Q_e, etc. can be calculated, and the net amount of heat passing through the sea surface determined. It is also necessary to know the depth of the layer absorbing the radiation and the quantity of heat brought into the surface layer by entrainment.

Consider the basic structure of an inlet to be that shown schematically in Fig. 3, where an upper brackish layer overlies a lower layer. The origin of the co-ordinate system is taken at the head of the inlet, with x directed along the inlet to seaward, y across, and z vertically downward. In the development which follows, the quantities in all cases refer to mean values for the water column within each layer.

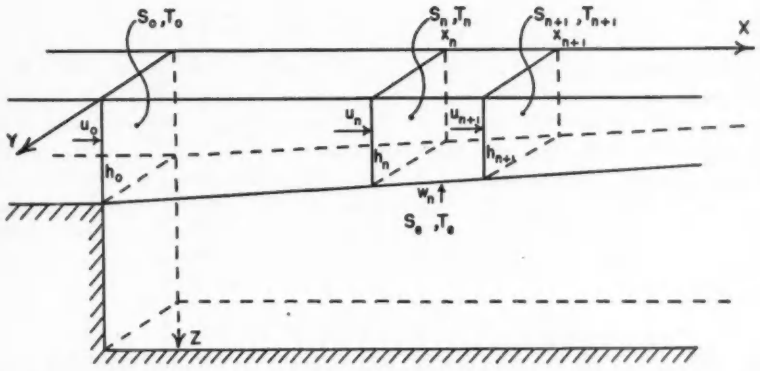

FIG. 3. Model of structure in upper layers of inlet for use in connection with heat budget study.

Consider a column of water at $x = 0$, with unit width and depth h_0. Suppose it to have a velocity u_0 in the x direction, a salinity S_0 and temperature T_0. The water column is described at x_n by the quantities u_n, S_n, T_n, and h_n. S_e and T_e are the salinity and temperature of the lower layer at any point. Assume that the net rate of heat flow through a unit area of sea surface is constant with time and position and is equal to Q cal./cm.^{2}/sec. ($Q = Q_s - Q_b - Q_e - Q_h$).

If a steady state is assumed the conservation principles may be applied to the column between x_n and x_{n+1} (Fig. 3) as follows:

Conservation of volume:

$$h_{n+1}u_{n+1} - h_n u_n - w_n(x_{n+1} - x_n) = 0 \qquad (2)$$

where w_n is the mean vertical velocity of entrainment from below. If the transport $hu = V$, and $w_n(x_{n+1} - x_n) = V_{en}$, then equation (2) may be written:

$$V_{n+1} - V_n - V_{en} = 0 \qquad (2a)$$

Conservation of heat:

$$T_{n+1} V_{n+1} - T_n V_n - T_e V_{en} = \frac{Q}{c}(x_{n+1} - x_n) = \frac{Q}{c} \cdot \Delta x \tag{3}$$

where c = specific heat of sea water.

Conservation of salt:

$$S_{n+1} V_{n+1} - S_n V_n - S_e V_{en} = 0. \tag{4}$$

Substituting V_{n+1} from equation (2a) into equations (3) and (4) yields:

$$T_{n+1} (V_n + V_{en}) - T_n V_n - T_e V_{en} = \frac{Q}{c} \cdot \Delta x \tag{5}$$

and

$$S_{n+1} (V_n + V_{en}) - S_n V_n - S_e V_e = 0. \tag{6}$$

Eliminating V_{en} between these equations yields:

$$\frac{T_{n+1} - T_n}{T_{n+1} - T_e} + \frac{S_{n+1} - S_n}{S_e - S_{n+1}} = \frac{Q \cdot \Delta x}{h_n u_n c(T_{n+1} - T_e)}. \tag{7}$$

This equation can be applied to the field data in two ways: First, if the salinity and temperature of entrained water are known, the velocity u_n of the water entering the section can be calculated. By applying this equation at the head of the inlet the inflow of fresh water may be determined. In principle, the equation also can be applied all the way down the inlet to determine the velocity at each point. Second, if the velocity of the surface layer is known, a relationship between the temperature and salinity of the entrained water is given. If all quantities but T_e and S_e in equation (7) are known, then the equation is of the form

$$T_e = C_1 + C_2 S_e \tag{8}$$

which indicates a linear relationship between the possible temperatures and salinities of entrained water. The depth from which it is drawn can be determined by plotting equation (8) on the same graph as the T–S curves for the stations of the inlet in question. The point where the straight line crosses the T–S curve represents an upper limit to the acceptable depths. The application of this technique will be illustrated later in this paper.

The form of equation (7) is suitable for the numerical calculations to be described later, but an alternative form which lends itself to a simple geometrical interpretation on a T–S diagram can be derived by substituting the expression for V_{en} from equation (2a) into equations (3) and (4) yielding:

$$(T_{n+1} - T_e) V_{n+1} - (T_n - T_e) V_n = \frac{Q}{c} \cdot \Delta x \tag{9}$$

and

$$(S_{n+1} - S_e) V_{n+1} - (S_n - S_e) V_n = 0. \tag{10}$$

Eliminating V_{n+1} yields:

$$\frac{T_{n+1} - T_e}{S_e - S_{n+1}} = \frac{T_n - T_e}{S_e - S_n} + \frac{Q \cdot \Delta x}{h_n u_n c (S_e - S_n)}. \tag{11}$$

If on a T, S diagram (Fig. 4) the points B (T_n, S_n) and D (T_{n+1}, S_{n+1}) represent the characteristics of the water column at x_n and x_{n+1}, and T_e, S_e are those of the entrained water, then:

$$\frac{T_{n+1} - T_e}{S_e - S_{n+1}} = \tan \alpha_{n+1} \text{ and } \frac{T_n - T_e}{S_e - S_n} = \tan \alpha_n$$

and equation (11) may be written:

$$(S_e - S_n) \tan \alpha_{n+1} = (S_e - S_n) \tan \alpha_n + \frac{Q.\,\Delta x}{h_n u_n c}; \qquad (11a)$$

i.e. in Fig. 4: $CA = CB + BA$,

while T_e, S_e may be anywhere on a straight line (AD produced down to the right in Fig. 4) as indicated in equation (8).

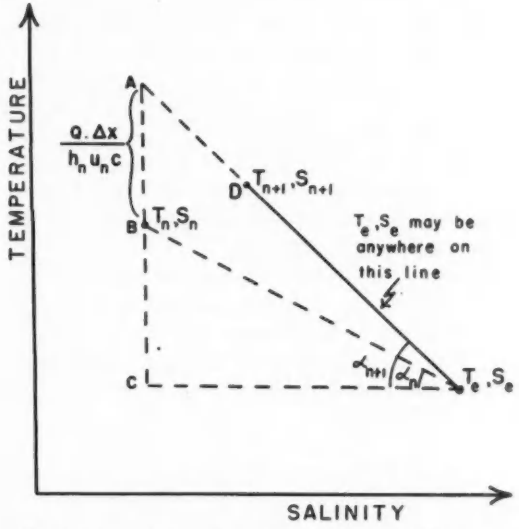

FIG. 4. Interpretation of equation (11) on T–S diagram.

The above development of equations (7) and (11) considers only entrainment upward. If there is downward penetration of fresh water into the lower layer then the conservation equations (2), (3) and (4) will be modified. These modifications were made and the new equations derived. Numerical tests showed that over most of the length of the inlet, downward penetration was small and hence the simple equation (7) for entrainment was considered adequate and only the results from its application are reported here.

There are a few points which should be noted when applying the physical data to the equation derived.

(a) A knowledge of the depth of no net motion is required. The direct current measurements that have been made in the inlets indicate that this depth

corresponds approximately to the halocline and thermocline depth (Trites, 1955). Thus in the upper reaches of an inlet it is particularly easy to locate the depth of no net motion because the halocline and thermocline are very clearly defined.

(b) The equations are all written for unit width and are applied without reference to inlet width. This implies that the actual width remains constant. In certain instances this is not the case, but for the majority of the British Columbia inlets the width is nearly uniform throughout the lengths where the equations have been applied. Available observations indicate that there is little variation in temperature or salinity across an inlet.

(c) Near the heads of the inlets the salinity of the surface layer is very low, and the increase (in absolute value) in salinity between stations in the upper reaches of the inlets is small. That is, only a very small proportion of water is being entrained. Consequently, when applying equation (7) only a small error is introduced if incorrect values are chosen for the salinity and temperature of the entrained water. However, as one examines the profiles to seaward, the importance of entrainment becomes very apparent, and the temperature and salinity of entrained water need be known more accurately. Therefore, since the velocities calculated for the upper reaches of an inlet appear quite reliable, these values may be applied to equation (7) for regions where entrainment is important to determine the depth from which the water is drawn. This information is likely to be of considerable value in studying the process of mixing, both from the physical point of view and also in connection with the maintenance of such features as plankton populations.

(d) The accuracy of the results depends upon the accuracy of the Q values used and it is difficult to assess this accuracy without direct measurements of the component heat flows. It is estimated that the Q values determined in the manner described above may be accurate to about $\pm 25\%$. Direct measurements might improve the accuracy but it is doubtful if the effort involved would be economic.

APPLICATION OF THE METHOD

Discharge

On the basis of equation (7), mean fresh water discharge values near the head were calculated for a number of the inlets at different times. These are summarized in the accompanying Table, and are compared with the discharge figures calculated from precipitation and river discharge measurements. In some instances, values for T_e and S_e have not been entered because there was no significant increase in salinity of the surface layer between the observation positions.

As mentioned previously, only a small number of the many rivers flowing into the inlets are or have been metered. Similarly, precipitation observations are limited. However, by combining both river discharge measurements and precipitation figures, it was possible to calculate the mean monthly runoff figures for all watersheds which drain into the inlets (Trites, 1955). This technique is quite independent of the heat budget method, and therefore it is of value to use

Fresh water discharge calculated from heat budget analysis (cu. ft./sec.).

Inlet	Date	Data from* station numbers	h_n	T_e	S_e	u_n	Fresh water discharge (from heat budget)	Fresh water discharge (from precipitation and runoff data)
			metres	°C.	‰	*cm./sec.*	*cu.ft./sec.*	*cu.ft./sec.*
Portland	22–25/vii/51	14–21	8.0	7.0	26.0	3.0	19,300	14,460
Portland	22–25/vii/51	12–9	7.0	8.0	25.0	3.2	—	—
Gardner Canal	2–3/vii/51	14–13	7.0	8.7	29.5	12.1	27,400	20,000
Gardner Canal	2–3/vii/51	13–12	6.5	6.7	29.5	10.3	—	—
Gardner Canal	2–3/vii/51	12–11	6.25	6.7	29.5	6.5	20,300	—
Gardner Canal	2–3/vii/51	11–9	6.0	6.7	29.5	7.0	—	—
Gardner Canal	2–3/vii/51	9–7	5.25	6.7	29.5	11.2	24,600	30,200
Gardner Canal	2–3/vii/51	7–6	5.0	6.7	29.5	13.1	—	—
N. Bentinck	22/vi/51	11–10	5.5	9.6	27.5	3.6	12,500	12,100
S. Bentinck	23/vi/51	15–13	9.0	9.9	26.0	4.4	17,700	8,140
Rivers	16/vi/51	5–4	3.5	8.1	27.5	4.8	15,000	12,700
Toba	9/vi/54	3–2	2.0	12.6	26.0	10.0	9,600	16,450
Bute	17–24/v/51	7–4	4.5	3.6	27.5	4.6	19,800	18,800
Bute	17–24/v/51	4–2	3.5	11.2	23.5	5.3	—	—
Bute	10–12/viii/52	7–6	5.3	9.2	25.0	3.1	16,100	15,300
Bute	10–12/viii/52	6–4	5.3	—	—	3.2	—	—
Bute	1–2/vii/53	6–4	3.0	—	—	7.6	22,000	24,600
Bute	20–23/viii/53	7–4	6.7	9.5	27.5	5.4	—	—
Bute	20–23/viii/53	4–2	4.9	—	—	9.8	16,600	15,300
Knight	3–4/vi/51	11–10	7.0	10.0	15.0	1.7	14,500	22,300
Knight	3–4/vi/51	10–9	7.0	10.0	15.0	5.6	37,500	22,300
Knight	3–4/vi/51	11–9	7.0	10.0	15.0	2.7	21,700	22,300
Knight	17/vii/53	11–10	5.5	—	—	3.0	19,440	16,200

*Note: Station numbers in each inlet start from 1 at the mouth and increase toward the head.

it as a check. The agreement between the figures (average difference 25%) is considered to be good, since those calculated from precipitation and river discharge measurements are only monthly averages, and values for a particular year are not obtainable until precipitation data are available, whereas those calculated from the heat budget represent an average over a few days at most, and for a specific year.

Calculated volume transports were also compared with those determined from available direct current observations (Trites, 1955). These measurements usually were made at only one position at a time, in the inlets, and only for a few of them. The mean values computed compared favourably with those derived from the heat budget analysis.

Depth of Entrainment

In order to demonstrate the method of applying equation (8) to the T–S diagram to indicate the depth from which the entrained water is drawn, observations from Knight Inlet will be considered.

The salinity and temperature profiles for three stations in the inlet on June 3–4, 1951, are shown in Fig. 5a and 5b. In Fig. 6, T–S curves are plotted for

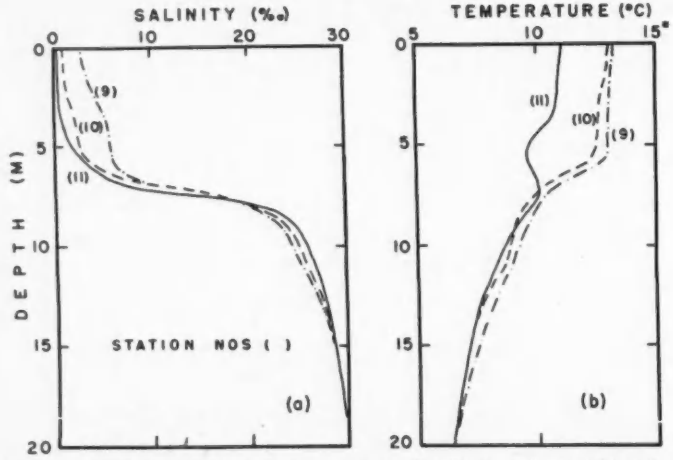

Fig. 5. Typical salinity and temperature distributions in Knight Inlet during summer.

stations 9, 10 and 11. A calculation (using equation 7) for the mean velocity of fresh water at the head of the inlet gives a value of 2.4 cm./sec. Applying this result, together with the Q of 0.224 cal./cm.^{2}/min. appropriate to the meteorological conditions at the time, and the observed values of h, T, and S at stations 9 and 10, gives a straight line as shown in Fig. 6. This indicates that entrained water must be drawn from a depth of 7 metres or more. This analysis was carried out for other stations down the inlet and also for other inlets and for other seasons, and some of the results (T_e, S_e, h) are given in the Table.

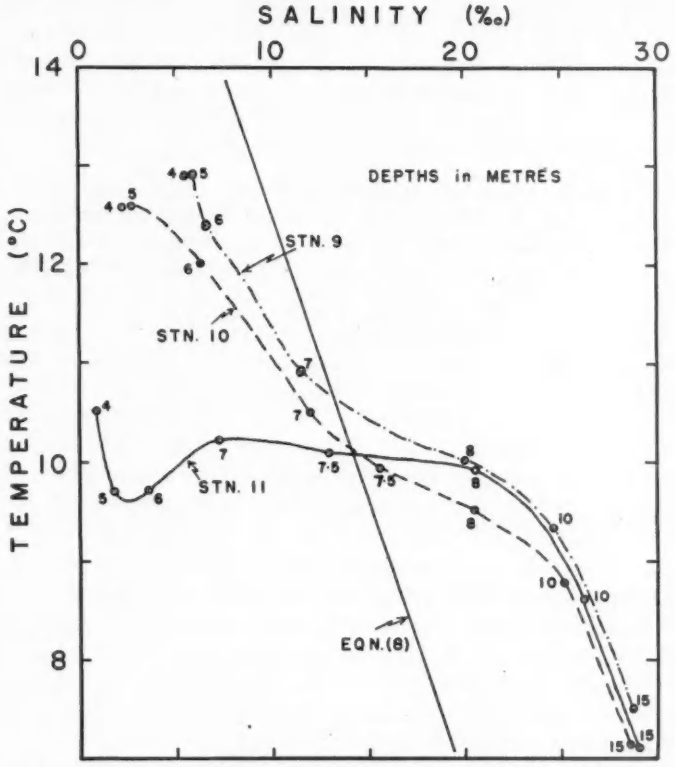

FIG. 6. Temperature, salinity curves for stations 9, 10 and 11 in Knight Inlet, and plot of equation (8) for this region.

It should be pointed out that errors in the estimation of Q will change the position of the line representing equation (8) on the T–S diagram (Fig. 6) and may thereby change the value of T_e and of S_e (particularly the latter) in the upper and middle reaches of an inlet. However, the change in the *depth* of entrainment is much less because of the large rate of change of T and S in the thermocline–halocline zone.

The results of the analysis indicated that generally the depth of no net motion decreases to seaward. This was required if the conditions on T_e and S_e in equation (7) were to be met. The major part of the up-inlet motion was found to be confined to a fairly narrow range of depth immediately below the depth of no net motion. The results also indicated that the salinity of the entrained water usually *decreases* slightly to seaward. It implies that in some region beyond the stations considered, i.e. toward the mouth, mixing downward must become important. It seems that possibly this is associated with the region of development of the critical velocity suggested by the studies of Cameron (1951) and

Stommel (1952), and that this occurs near the mouth of the inlet. Up-inlet from this position, the predominant vertical process across the level of no net motion is entrainment of salt water from below (i.e. a uni-directional flow upward). This conclusion has also been drawn by Tully (1949) in studies of Alberni Inlet. However, to seaward of the position where the critical velocity exists, exchange processes (i.e. both upward and downward flow) may predominate.

CONCLUSION

The application of the heat budget method for the determination of net transport in the surface layer gives results which are in good agreement with those derived from fresh water discharge analysis. The method offers some very real advantages over direct methods for determining fresh water inflow and circulation. The accumulation of fresh water in the inlets effectively acts as a smoothing device in determining the mean fresh water discharge over a period of a few days, the period depending on the inlet size. Another advantage is that the method permits the determination of net currents without the necessity of anchoring a vessel. Although a number of temperature, salinity, and meteorological observations are necessary, the effort required, both in time and equipment, to give a reliable value for the net current is considerably smaller than is required for direct current measurements.

ACKNOWLEDGEMENT

The authors wish to acknowledge with thanks the assistance of the Fisheries Research Board of Canada through its Pacific Oceanographic Group, Nanaimo, B.C., during the preparation of this paper, the assistance of the National Research Council of Canada through research grants, and of the Royal Canadian Navy through the provision of research vessels during the collection of field data upon which the numerical calculations are based.

Equation (7) was originally derived from a Lagrangian point of view. The authors are grateful to Dr. N. P. Fofonoff of the Pacific Oceanographic Group for suggesting the neater Eulerian derivation presented above and for pointing out the alternative form (equation 11) and its interpretation on the T–S diagram.

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The Action of *Pseudomonas* on Fish Muscle: 1. Organisms Responsible for Odours Produced During Incipient Spoilage of Chilled Fish Muscle[1]

By C. H. Castell and Maxine F. Greenough

Fisheries Research Board of Canada
Technological Station, Halifax, N.S.

ABSTRACT

Many of the odours characteristic of the earlier stages of spoilage of chilled fish muscle have been reproduced by inoculating sterile fish and fish media with pure cultures of bacteria isolated from fish. These organisms belong to the *Pseudomonas* and the majority are neither proteolytic nor break down trimethylamine oxide. They are chiefly achromogenic, although a few green pigmented species are included. Odour production by these organisms appears not to be inhibited by sodium nitrite. Similar odours, produced by similar types of organisms, have been observed in the past on dairy products, eggs, meat, poultry and other protein foods held in cold storage.

INTRODUCTION

Odours of Spoiling Fish Muscle

It has been observed that during the spoilage of fish muscle there is often a tendency for particular odours to develop in a fairly regular succession, producing easily recognized spoilage patterns (Elliott, 1947; Castell and Anderson, 1948; Dyer and Dyer, 1949; Shewan *et al.*, 1953).

In their attempt to develop a scoring system for the assessment of spoilage in white fish, Shewan and his co-workers (1953) have listed many of the characteristic odours and the relative order in which they are formed (Table I). It

Table I. The odours of raw and cooked white fish taken from the score sheet of Shewan *et al.* (1953), in their attempt to develop a scoring system for the sensory assessment of spoilage of wet white fish stored in ice.

Odours	Score
From raw fish	
Fresh 'seaweedy'	10
Loss of fresh 'seaweediness', shellfishy	9
None or neutral	8
Slight musty, acetamide-like, milky or caprylic acid-like	7
'Bready', 'malty', 'yeasty'	6
Lactic acid, 'sour milk', or oily	5
Some lower fatty acid (e.g. acetic or butyric acids), 'grassy', slightly sweet, or fruity	4
Stale, sour, 'cabbage water', 'turnipy', or phosphine-like	3
Ammoniacal (trimethylamine and other lower amines) plus strong *o*-toluidine-like	2
Hydrogen sulphide, other sulphide and strong ammoniacal	1
Nauseating, putrid, faecal; indole, ammoniacal, etc.	0
From cooked fish	
Strong fresh 'seaweedy'	10
Some loss of fresh 'seaweediness'	9
Lack of, or neutral	8
Slight strengthening, but not sour or stale; 'wood shavings', 'woodsap', vanillin or terpene-like; slight salt-fish or cold storage-like	7
'Condensed milk', caramel or toffee-like	6
'Milk jug', 'boiled-potato' or 'boiled clothes', or metallic	5
Lactic acid, 'sour milk' or *o*-toluidine-like	4
Some lower fatty acid (e.g. acetic or butyric acids), 'grassy', 'soapy', 'turnipy' or 'tallowy'	3
Ammoniacal (trimethylamine and lower amines)	2
Strong ammoniacal (trimethylamine, etc.) and some sulphide	1
Strong putrid and faecal (ammonia, indole, etc.)	0

[1]Received for publication November 14, 1956.

J. Fish. Res. Bd. Canada, 14(4), pp. 617–625, 1957.
Printed in Canada.

would indeed be a rare fish that successively developed all the odours listed in their table; but at one time or another most of these same odours have been encountered in the muscle of cod, haddock, flounder or halibut on the Canadian Atlantic coast, and the general order in which they develop agrees well with the British observations.

In reference to the development of odours, it is convenient to divide the spoilage of chilled fish muscle into four stages, all of which are included in Shewan's table.

First stage. Muscle cut from all fresh fish has a characteristic odour which varies slightly with different species. For want of a better term this has been called "fresh fish odour", "sea fresh tang".

Second stage. This is characterized chiefly by the loss of some of the normal, fresh fish odour without the development of any spoilage odours. For this reason it is frequently referred to as the "neutral" stage.

Third stage. This begins with the development of the first spoilage odours. Here there is a considerable variation, particularly during the different seasons of the year. Occasionally the first noticeable odour is "sweet" or "perfume-like", suggesting the delicate odour of certain chemical esters found in fresh fruits. This usually develops into odours characteristic of sour or fermenting fruit.

A second variation of this third stage includes various odours suggestive of fresh and spoiling vegetables (particularly *Cruciferae*). Less frequently this may be accompanied by musty, potato- and garlic-like odours. There are many other odours that may occur during this stage, and while they are not necessarily pleasant, they are not of the highly offensive types which develop later.

Fourth stage. In the last stage, the odours become stronger and more offensive and the fish is usually described as bad, rotten, putrid or faecal. Here again there is a considerable variation, probably depending upon the presence and proportion of trimethylamine, hydrogen sulphide, ammonia, indole, etc., produced during this last stage of spoilage.

Some of the earlier studies of the bacterial breakdown of the muscle of many species of marine fish indicated that it took place in two well-defined but overlapping stages. The first was the reduction of trimethylamine oxide to trimethylamine, coupled with the oxidation of lactic acid and certain carbohydrates. The second was the hydrolysis and subsequent decomposition of the proteins. The odour of the fish in the earlier stage was attributed chiefly to trimethylamine and in the later stage to the end products of protein breakdown. This hardly agrees with the picture of spoilage indicated by the development of the spoilage odours. According to Shewan's table the odour of trimethylamine becomes apparent after the fish has reached the stage where it should be scored 2 out of 10 in an organoleptic rating, and after the fish had already passed through several previous stages of spoilage. It has also been pointed out by Castell and Triggs (1955) that although traces of trimethylamine may accumulate in the muscle, it will not add to the spoilage odour until the pH of the fish has increased to the point where this amine can be released as a free base.

The truth of the matter is that the two overlapping stages mentioned above

may have little or nothing to do with the odours developed during the earlier stages of the spoilage of fish muscle. It can be shown, as will be pointed out in this paper, that many of these odours are caused by bacteria that neither reduce trimethylamine oxide nor hydrolyze proteins.

This paper is concerned with these bacteria that produce the odours so frequently met with during the incipient stage of spoilage, before the fish has reached the unmerchantable condition. To begin with it describes the organisms as a group and discusses their general relationship to spoilage. After that it deals in greater detail with some of the more representative cultures that are responsible for the production of specific spoilage odours.

EXPERIMENTAL

Source of the Cultures

Most of the cultures were isolated from agar plates that were being used for making routine counts on fresh and spoiling cod, haddock, halibut and flounder. A few were from plates purposely poured from fillets having a very characteristic odour. A few also were from ice and the water supplies from fish plants.

The cultures selected for study from many hundred isolates were those which produced characteristic odours or series of odours when inoculated into sterile fish medium. Particular interest was taken in obtaining cultures which produced odours similar to those encountered in the earlier stages of spoilage of chilled fillets.

From the original isolates, 135 were selected for detailed study. The purpose of this second selection was to eliminate most of what were obviously similar strains or species. Even after this reduction in numbers, it seemed apparent that there were not more than fifteen or twenty distinct strains or species.

A general description of all the organisms included in the group studied is as follows: gram-negative rods; non-motile or motile with polar flagella; many producers of green or blue-green fluorescent water-soluble pigments; those having no pigments. They are generally inactive in fermenting sugars and other carbohydrates, although they produce acid, but not gas, from dextrose. All produce catalase. They are aerobic and tend to be psychrophilic; most of the cultures show little or no growth at 37° C.; many grow better at 10 to 15° C. than at 25° C.; most grow slowly at 0 to 2° C.

Identification of Cultures to Genera

The initial object was to classify the organisms as far as their genera. It first appeared that the cultures consisted of *Pseudomonas* and *Achromobacter*. During this preliminary work, the characteristic water-soluble blue and green pigments were used as the basic characteristic in the identification of *Pseudomonas*. Later, however, when flagella strains were made, it was found that all the motile achromogenic cultures had polar flagella and therefore belonged to the *Pseudomonas*. The remaining, non-motile achromogenic cultures could have been classified as either *Achromobacter* or *Pseudomonas* according to Bergey's Manual

of Determinative Bacteriology, but as they fell into a uniform group with the other cultures it was decided to classify them all as *Pseudomonas*. There is no explanation as to why other genera, commonly associated with fish and fish spoilage, were not encountered in this collection, except that the method of selection may have eliminated them.

Methods

Except where stated otherwise, standard methods have been used. Flagella were stained by the method outlined by Oliver (1934). The incubation temperature for initial isolations and for studying cultural characteristics was 25° C. Trimethylamine determinations were made by Dyer's colorimetric test (1945, 1950). The ability of a culture to reduce trimethylamine oxide was tested by the technique of Wood and Baird (1943) and the ability to produce trimethylamine from choline, by the method of Wood and Keeping (1944). The medium for the reduction of nitrate to nitrite and also the reduction of nitrite itself was that suggested by Liu (1953). Hydroxylamine was measured by the method of Novak and Wilson (1948). Urease activity was tested by the technique suggested by Tidwell *et al.* (1955).

RESULTS

Odours on Fish from Pure Cultures

In order to determine the characteristic odours produced on fish by the organisms studied, pure cultures were repeatedly inoculated onto sterile fish muscle and fish media, and observed periodically. The muscle used was from cod and haddock. Some tests were made with unheated, aseptically removed muscle, but the difficulties involved in producing the hundreds of sterile samples that were required led to the use of heat-sterilized muscle in closed glass containers. Almost all the characteristic odours produced by these organisms on sterile, unheated fish muscle were also produced by the same organisms on heat-sterilized muscle or autoclaved fish media.

Other tests were made by inoculating the surface of sterile fish muscle blended in agar and poured in sterile petri plates. Each culture was grown on one or more of these fish substrates at least six times and the odours were observed; some of the more interesting types were repeated twenty or thirty times over a period of 5 years. Table II is a summary of the typical odours that were encountered. It will be noted that very few of the cultures produced single persisting odours. There was usually a series of two to four successive odours with one predominating.

To persons not accustomed to exploring characteristic odours of spoiling fish, many of the descriptive terms used in Tables I and II may sound rather prosaic. But, as stated by Shewan *et al.* they are the terms spontaneously used and agreed upon by the panels or persons assessing the fish. Although not very scientific, these terms are readily recognized by most persons who have had experience in examining and grading sea fish in various stages of deterioration.

It is interesting to observe that most of the odours produced by these cultures of *Pseudomonas* on fish muscle are more suggestive of fresh and spoiling

TABLE II. Odours produced on cod and haddock muscle by pure cultures of *Pseudomonas* isolated from fish and marine environments.

Little or none
'Sweet', 'like amber honey', 'perfume-like', 'maple syrup'
Sweet > musty > fruity
Fruity > sour fruity > garlic or oniony > rotten onions
Musty > the smell of stored potatoes > ammonia and potatoes
Potatoes > sour fruity
Strong celery odour > fruity > sour fruity
Musty
Fruity > sour fruity > putrid and ammonia
Sweet > fruity > sour kitchen drain > spoiling cabbage
Sour vegetables, old cabbage water
Mustard > mercaptan > putrid
Raspberry 'stink-bug' (*Pentatomidae*)
Sour vegetables > putrid
Slightly putrid, musty putrid > decomposing cabbage
Scorched paper > mustard > mercaptan

fruit and vegetables than they are of the odours that we usually associate with decomposing flesh.

Among all the various odours and combinations of odours there were some that predominated and could be easily reproduced with the pure cultures on the fish muscle. These odours were quite typical of the *Pseudomonas* as a group. Their variety included sweet, fruity, sour or fermenting fruit, oniony, onion-pickles and rotten onions, mustard, musty, potatoes, cabbage, cabbage-water, rotten cabbage, sour vegetables, sour kitchen drainpipe, methyl mercaptan, stink-bug (*Pentatomidae*, raspberry stink-bug), and putrid. It can be seen that they represent quite a large proportion of the odours listed by Shewan *et al.* (Table I) as occurring during the various stages of the spoilage of chilled white fish.

Tests for the production of odours were made with inoculated fish muscle and fish media held at 0° C. (32° F.), 2° C. (36° F.), 7° C. (45° F.), 20 to 25° C. (68 to 77° F.); still others were held at 0° C. for several days and then transferred to room temperature, approximately 25° C. (77° F.).

All the characteristic odours listed above were produced at all temperatures ranging from 0 to 25° C., but much sooner at the higher temperatures (10 to 25° C.). At 0 to 2° C. there was a greater variation in the rate of odour production among individual cultures; many cultures producing a succession of odours reached the last stage in 2 to 3 days at 25° C., whereas they were often at the initial stage after a week or more at 0 or 2° C.

There was a small proportion of cultures that grew on the fish but produced little or no odour; another small group produced mild odours which subsequently disappeared.

Over a period of several years it was observed that most of the cultures lost their ability to produce their characteristic odours after repeated transfers on agar media. Sometimes, but not always, this ability could be restored by growing them on suitable substrates. This was particularly so of the sweet and fruity types. Others, including the "potato" odour cultures, retained their characteristic odour after repeated transfers over a period of 6 years.

ODOURS *VS.* CULTURAL CHARACTERISTICS

An attempt was made to determine whether any correlation could be found between the common cultural characteristics that are ordinarily used in identifying bacteria, and the odours produced by the organisms on fish muscle. The tests included: hydrolysis of proteins; gelatin liquefaction; the production of indole, hydrogen sulphide, mercaptans and ammonia from appropriate substrates; hydrolysis of fats, lecithin and simple triglycerides; the action on various sugars and carbohydrates in both open and sealed tubes; the reduction of nitrate and nitrite; the formation of nitrite from hydroxylamine; hydrolysis of starch and decomposition of cellulose; the reduction of trimethylamine oxide and the production of trimethylamine from choline; pigment production and fluorescence under ultraviolet light.

The tabulation of the results of these tests for so many cultures produces a very large table, but yields relatively little information on their relation to odour production. The one and only significant observation is the relation between proteolytic activities of the bacteria and the types of odour they produce. All those cultures that produce predominantly sweet, fruity, oniony and potato-like odours are non-proteolytic and the majority are non-pigmented. Those that produce odours of spoiling, *Cruciferae*, mercaptans, stink-bug, and other putrid odours are proteolytic and pigmented. Some of these "stinker" types may initially produce transient ester or fruit-like odours but they rapidly change into the more offensive types. However, proteolysis was not the sole determining factor in the production of these rotten and putrid odours. Some cultures were encountered that were definitely proteolytic, but produced either no odour, or mild musty or sour odours. Generally these particular cultures exhibited little or no action on simpler nitrogen compounds, suggesting that the *degree* of protein decomposition, rather than the initial hydrolysis, is the important consideration.

There appeared to be no correlation between the odour produced on fish and any of the other cultural characteristics used in testing these organisms. Further details will be given in the subsequent study of the bacteria concerned with particular characteristic odours.

FRUITY ODOURS ON COMMERCIAL FISH

From several years of experience in examining and grading fish, there are a few general observations that are related to these fruity odours. They appear to be more prevalent in the fall, winter and early spring than in the warmer seasons of the year. They have been encountered on flat fish as well as groundfish. They are encountered much more often on fillets than on round, gutted or dressed fish. They have also been observed on fillets at every stage from the fish plant until they have reached the consumer in the inland markets.

Fresh fillets shipped from the eastern Atlantic provinces are usually given a preservative dip in sodium nitrite before packing. Such fillets spoil more slowly than untreated fillets, and with a different spoilage pattern. The chief difference is that the third spoilage stage—the period when these sweet, fruity

TABLE III. The odours observed during the spoilage of two similar lots of cod fillets held at −0.5° C. (31° F.). One lot had been dipped in a 0.2% solution of sodium nitrite prior to going into storage.

Days in storage	Odours	
	Control fish	Treated fish
0	Fresh	Fresh
4	Slightly fruity	Not much odour
7	Fruity and sour-fruity	Sweet-fruity
9	Putrid	Fruity
11	Strongly putrid	Strongly fruity
14	" "	Very strongly fruity
18	" "	" " "
22	" "	" " "
29	" "	Strong fruity and putrid

and less offensive odours predominate—is prolonged and intensified. This can be seen from a very typical set of observations given in Table III. In 6 and 9 days the untreated fillets changed from fruity to putrid. During this same period the odour of the treated fillets became more intense but not putrid. At a somewhat later stage the graders characterized it as "sickeningly fruity". It was not until after 4 weeks' storage that the typical putrid odours became evident.

This is not unexpected, as it has been demonstrated that nitrite may inhibit specific enzyme reactions such as the reduction of trimethylamine oxide to trimethylamine (Castell, 1949) and the reduction of organic sulphur compounds to hydrogen sulphide (Richards, 1951) which contribute to the fourth or putrid stage of spoilage. Tests with pure cultures of organisms giving rise to fruity and potato-like odours have shown that in the concentration used on fish, nitrite does not interfere with the production of their characteristic odours.

DISCUSSION

In the past, many workers classifying bacteria associated with fish and fish spoilage have used the presence of the green or blue-green pigments as the basic characteristic in the identification of *Pseudomonas* (Reed and Spence, 1929; Gibbons, 1934; Gee, 1930; Snow and Beard, 1939; Wood, 1940; Aschehoug and Vesterhus, 1947; Dyer, 1947). This tendency to use pigmentation as the primary characteristic in identifying *Pseudomonas* is not restricted to the fishery bacteriologists. As pointed out by Gaby and Free (1953), many clinical bacteriologists have done the same. In this connection it is interesting to note that at least nineteen species now recognized in Bergey's (1948) Manual as being in the *Pseudomonas* were at one time or another classified as *Achromobacter*. This applies particularly to those species listed as "green fluorescent pigment not produced or not reported". One cannot help but wonder whether many of the *Achromobacter* so frequently associated with fish in earlier studies may not have been achromogenic *Pseudomonas*. This present work indicates that these latter organisms are quite common among the isolates from chilled fish muscle.

It is also interesting to note that odours similar to those described above have previously been observed developing in chilled foods other than fish. In

many instances the causal organisms have also been identified as *Pseudomonas*. In his most interesting paper on "Aroma-producing micro-organisms" Omelianski (1923) surveys the work of early European bacteriologists in this field. Even before the turn of the century many organisms had been isolated and studied that were capable of producing sweet, ester-like and fruity odours in meat-peptone bouillon as well as in milk and other dairy products. Jensen (1954), in a review of subsequent literature on this subject, with a particular reference to meats mentions organisms causing musty, earthy, weedy, ester-like, fruity and turnip-like odours. Jensen himself has encountered meat with "black walnut", "fruity", "weedy" and "musty" odours which were shown to be caused by cultures of *Pseudomonas* and *Achrombacter*. Similar odours have been observed in recent years in dairy products by American workers. Hussong, Long and Hammer (1937) isolated an organism which they identified as *Ps. fragi*, producing a sweet ester-like odour resembling the flower of the May-apple. Subsequently, Morrison and Hammer (1941) found it to be widely distributed in dairy products, soil, and plant water supplies. Turner (1927), Spanswick (1930), and Levine and Anderson (1932) isolated and identified, as either *Pseudomonas* or *Achromobacter*, organisms producing musty odours on eggs. Olson and Hammer (1934) isolated from dairy products similar organisms which they further described as producing a distinct potato-like odour. The causal organisms were identified as *Ps. graveolens* and *Ps. mucidolens*. Jensen (1954, p. 291) speaks of a culture which lost its ability to produce its characteristic musty odour on nutrient agar and in its place produced a faint fruity odour.

It would appear from these observations that many of the odours developing during the incipient stages of spoilage in chilled fish muscle are caused by various strains or species of *Pseudomonas*. It is also evident from the literature that similar odours, also caused by *Pseudomonas*, have been observed in milk, eggs, meat, poultry and other non-acid foods held in cool storage. Because many of these organisms neither hydrolyze proteins nor reduce trimethylamine, a further study of their activity on fish muscle might add significantly to our knowledge and control of the earlier stages of fish spoilage.

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Influence of Intermittent Short Storage Periods at 15°F., as Encountered During Refrigerator Car Transportation, on the Quality of Frozen Cod Stored at 0°F.[1,2]

By W. J. Dyer, Doris I. Fraser, D. G. Ellis and W. A. MacCallum
Fisheries Research Board of Canada
Technological Station, Halifax, N.S.

ABSTRACT

Frozen cod fillets subjected to a 2-week period of storage at 15° F. (–9.4° C.) after storage at 0° F. (–18° C.) for 1, 3, 6, and 9 months, with subsequent storage at 0° F., suffered considerable deterioration in quality as measured by taste panel and protein solubility tests. Frozen fish should not be transported at temperatures as high as 15° F.

INTRODUCTION

For many years fisheries technologists have been recommending that frozen fish should be shipped at temperatures lower than the 15 to 18° F. commonly encountered in Canadian refrigerator cars (Taylor and Harrison, 1948). These cars are cooled by means of an ice–salt mixture. Lower temperatures may be obtained by the use of eutectic mixtures of ice with other salts (Carbert and Cook, 1948; Carbert *et al.*, 1948), and by modifications to the bunker car design (Lentz and Cook, 1953; Cook *et al.*, 1951). Mechanical refrigerator cars capable of providing still lower temperatures have been developed in the United States and in Canada (Young *et al.*, 1948; Young, 1949; Young and Baker, 1951; Anon., 1950; Henney and McCoy, 1954), but the railways have asked for evidence of the necessity of these lower temperatures for transporting frozen fish.

The effect of storage temperature on the quality of fish in frozen storage has now been investigated for many species (Notevarp and Heen, 1940; Dyer, 1951 and 1953; Heen, 1953; Banks, 1954). The results of these investigations show that storage of frozen fish at temperatures of 0° F. or below is necessary to prevent serious deterioration. A survey of freezer storages in the United States by Munter, Byrne and Dykstra (1953) shows that temperatures of 0° F. or below are common. The same is true of the warehouses of many if not most Canadian fish processors.

However, the effect of exposure to higher temperatures for a period of 1 or 2 weeks has not been investigated previously. This paper reports such a study, using commercially frozen cod fillets.

EXPERIMENTAL

It was decided to employ cardboard cartons commonly used for frozen fillets. The master carton selected measured 12¾ by 9 by 8½ inches and held twenty-four

[1]Received for publication November 30, 1956.
[2]Paper No. 9 of a series "Proteins in Fish Muscle".

J. Fish. Res. Bd. Canada, 14(4), pp. 627–635, 1957.
Printed in Canada.

1-pound packages. The latter were of waxed cardboard holding 1 pound of fillets and were wrapped with waxed paper and machine sealed. In order to measure the rate of change of temperature in such a master carton, thermometers were placed in holes bored through the end of a full carton, with the thermometer bulbs positioned midway between the two sides and extending just short of centre. This master carton was equilibrated a few days at 0° F. and then transferred to a storage chamber averaging 13.5° F. This was thermostatically controlled, the air being circulated by a small fan. The results, shown in Fig. 1,

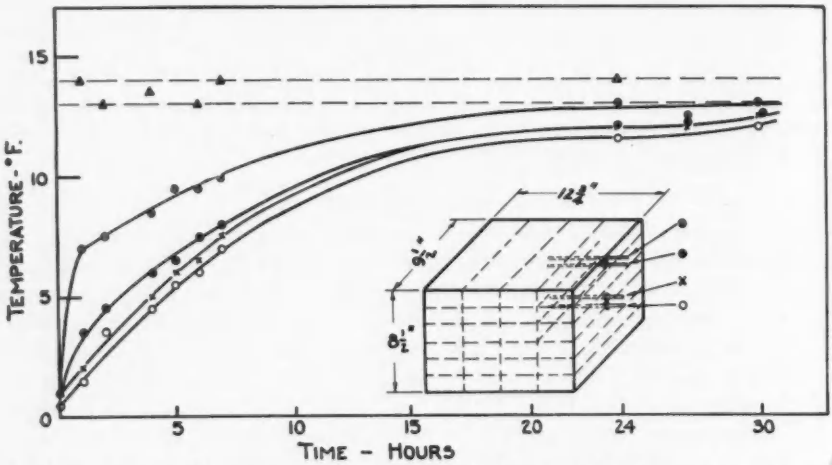

FIG. 1. Temperature changes in a carton of frozen cod when transferred from 0° F. (−18° C.) to 13.5° F. (−10.3° C.).

○—Centre of carton.
×—Block of fish next to centre.
●—Block of fish next to outside of carton.
△—Between carton and outside block.
⊙—Air temperature.

indicated that the temperature rose markedly in the first few hours and was not yet uniform even after 30 hours. The steepest temperature gradient was through the wall of the master carton and between it and the adjacent block of fish inside. There was very little temperature difference between the fish on the outside or in the centre of the carton. This simplified sampling in subsequent experiments, since all the 1-pound blocks should be about the same temperature. In practice, if the cartons were piled closely together, the temperature change should be slower; its duration would perhaps be more nearly the 4 or 5 days suggested by the data of Carbert, Rooke and Cook (1948). On the other hand, if the refrigerator cars were not properly precooled and the cartons were allowed to stand for a few hours during loading, the temperature rise might be accentuated.

For the experiment, fresh cod that had been in ice for 2 days on the vessel were filleted and packed as above and immediately frozen in plate freezers. The packages were then placed in master cartons, and transported to the laboratory where they were placed immediately in a constant temperature storage chamber at 0° F.

To ascertain the effect of short periods of storage at 15° F., as in shipment by refrigerator car, a box was removed after 1 month at 0° F., placed at 15° F. for 2 weeks and then returned to 0° F. Similarly, boxes were placed at 15° F. for 2 weeks after 3, 6, and 9 months at 0° F. This was to determine whether there was any difference in the effect, if the frozen fish were transported inland soon after packing or after storage in the Coast warehouses.

In addition, the effect of a possible second trans-shipment by refrigerator car was simulated. A carton of fish, which had been stored at 0° F. for 1 month after packing, was placed at 15° F. for a period of 2 weeks, then returned to 0° F. It was again placed at 15° F. for a 2-week period at 3 months after packing. Similarly, a carton, stored at 0° F. for 3 months, then at 15° F. for 2 weeks, and returned to 0° F., was again placed at 15° F. for a 2-week period at 6 months after packing.

The quality of the stored samples was checked periodically by taste panels (Dyer and Morton, 1956; Dyer and Dyer, 1949) and by protein solubility determinations (Dyer *et al.*, 1950; Dyer, 1951; Dyer and Morton, 1956). For the purpose of collecting data on other changes during storage, determinations were also made of moisture, total nitrogen, non-protein nitrogen, and free fatty acids (Dyer and Morton, 1956; Dyer *et al.*, 1950), trimethylamine and trimethylamine oxide (Dyer, 1945; Dyer *et al.*, 1952).

RESULTS

As found with rosefish (Dyer *et al.*, 1956), storage caused no change in the following analytical values determined in duplicate at monthly intervals: moisture, 80.6(±0.55)*%; total nitrogen, 2.83(±0.056)%; non-protein nitrogen, 0.35(±0.020)%; "albumin" (water-soluble protein) nitrogen, 0.57(±0.056)%; trimethylamine, 0.97 (±0.34) mg. N per 100 g. tissue; trimethylamine oxide, 59.8 (±8.2) mg. N per 100 g. tissue. The protein nitrogen was thus 2.48%, of which the albumin constituted 23%.

There was a small amount of drying out along the edges and ends of the blocks as storage proceeded, and there was no observable difference between the various treatments. There was no other visible change during storage.

Extractable Protein

The extractable actomyosin is shown in Fig. 2 and 3. The top line shows the decrease at 0° F. throughout, which is similar to earlier results (Dyer, 1951). However, sample B, placed at 15° F. for 2 weeks after 1 month at 0° F., showed a rapid drop beginning at 6 to 8 weeks, continuing to a level of only 0.9% actomyosin nitrogen at about 20 weeks, followed by a gradual decrease. It is evident

*Standard deviation of individual measurements.

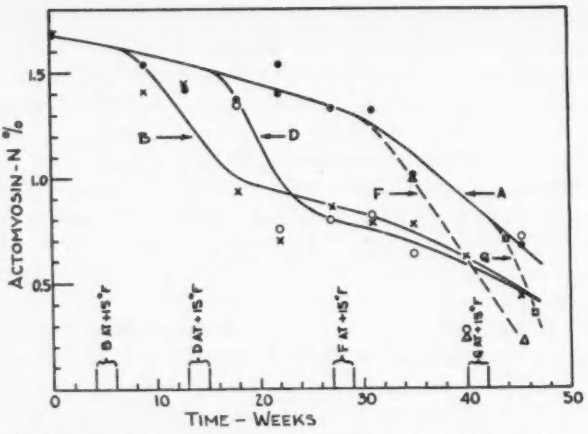

FIG. 2. Extractable actomyosin, as percentage N of fish, in stored frozen cod fillets.

- ● A—Stored continuously at 0° F. (−18° C.).
- × B—Stored at 0° F. for 1 month, then 2 weeks at +15° F. (−9.4° C.), and subsequently at 0° F.
- ○ D—Stored at 0° F. for 3 months, then 2 weeks at +15° F., and subsequently at 0° F.
- △ F—Stored at 0° F. for 6 months, then 2 weeks at +15° F., and subsequently at 0° F.
- □ G—Stored at 0° F. for 9 months, then 2 weeks at +15° F., and subsequently at 0° F.

that there has been a very significant decrease in protein solubility due to storage at 15° F. Similarly, samples D, F, and G, placed at 15° F. for 2 weeks, showed a rapid drop after 3, 6, and 9 months respectively at 0° F. Samples C and E, Fig. 3, which were placed at 15° F. twice, 2 and 3 months respectively after the first exposure, showed a further drop in solubility. These results on protein extractability show a very definite deterioration in quality due to the raising of the temperature to 15° F. for a 2-week period. Furthermore, the effect is still present whether the samples had been stored for 1 month or for 9 months at 0° F. before this treatment.

ORGANOLEPTIC SCORES

The taste panel scores on the cooked samples are shown in Fig. 4 and 5. In Fig. 4 the top line shows the scores for the sample stored continuously at 0° F. The grade dropped uniformly, the samples becoming unacceptable at about 40 weeks (i.e. 9 months). This agrees with our previous results. When placed at 15° F. for 2 weeks and returned to 0° F. storage, there was an immediate drop of almost 10% in the palatability scores, which drop persisted through the remainder of the storage period. At 3, 6, and 9 months, a similar drop occurred showing that the degree of deterioration was the same whether the storage at 15° F. for 2 weeks occurs at the beginning or near the end of the storage period.

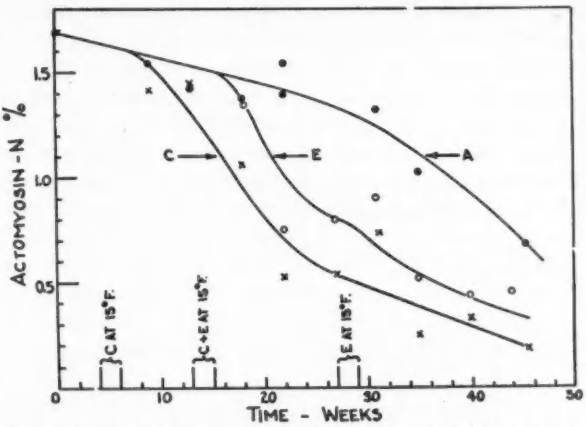

FIG. 3. Extractable actomyosin, as percentage N of fish, in stored frozen cod fillets.

● A—Stored continuously at 0° F.

× C—Stored at 0° F. for 1 month, then 2 weeks at +15° F., again at 0° F. for 7 weeks, then again at +15° F. for 2 weeks, followed by subsequent storage at 0° F.

○ E—Stored at 0° F. for 3 months, then 2 weeks at +15° F., again at 0° F. for 12 weeks, then again at +15° F. for 2 weeks, followed by subsequent storage at 0° F.

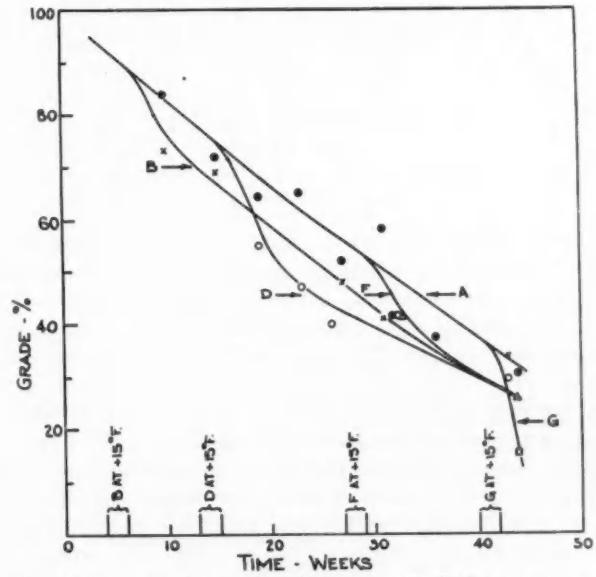

FIG. 4. Average taste panel grade in frozen cod fillets. (Legend as in Fig. 2.)

The changes are not quite as marked as those in extractable protein. The keeping time to unacceptability has been reduced to about 7½ months.

The effect of a second exposure to 15° F. is shown in Fig. 5. The sample placed at 15° F. at 1 month and again at 3 months showed a drop in grade of about 23% from the control which was kept continuously at 0° F. It had become unacceptable at just under 6 months (25 weeks). Similarly, the sample subjected to 15° F. at 3 months and at 6 months dropped in taste panel score, although not quite as much. It had become unacceptable at about 6¼ months (29 weeks).

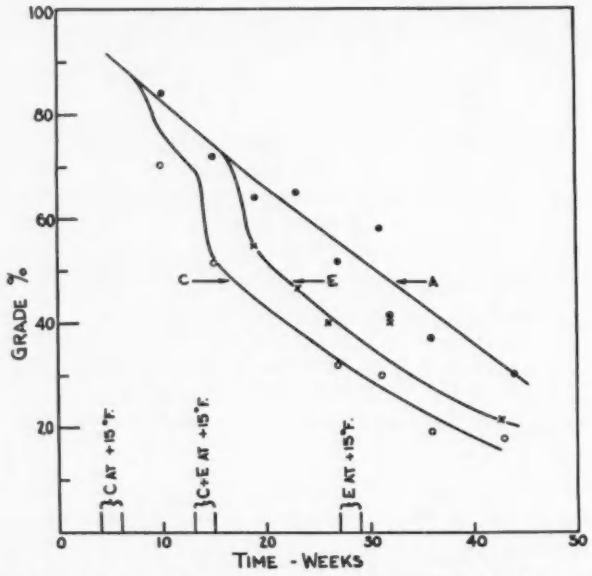

FIG. 5. Average taste panel grade in frozen cod fillets. (Legend as in Fig. 3.)

A few determinations of free fatty acid were made. At 10 weeks, the samples averaged 3.1%, expressed as percentage oleic acid in the extracted fat. At 21 weeks, the values had reached 60%, and were unchanged at 26 and at 33 weeks. These data are insufficient to be correlated with the other changes, as has been done with some other species (Dyer *et al.*, 1956), and this point is being investigated further.

In considering the rather large effect of short periods of storage at higher temperatures on protein extractability and palatability scores as shown by the results obtained, it is probable that there must be some additional factor causing a change in quality. The results of storage of frozen cod at temperatures of 10 and 15° F. did not indicate such a great difference in quality deterioration as found here (Dyer, 1953). Furthermore, experiments using storage temperatures fluctuating 5 or 10 degrees from the average temperature have shown no effect

differing significantly from that expected at the average temperature (striped bass and mackerel, Pottinger, 1951; beef and pork, Winter *et al.*, 1952; turkeys, Klose *et al.*, 1955). However, these experiments were conducted with an average temperature in the range of 0 to 5° F., whereas the temperature in the present experiment was up to 15° F. The amount of water in the salt solution in the tissue, which freezes out as ice, increases as the temperature is lowered. Data on the proportion of water frozen out at various temperatures in fish muscle are rather scarce. Finn (1934) determined the amount of ice frozen out from a halibut muscle press juice by separating the ice by filtration at successively lower temperatures. Mahadevan and Carter (1948) determined the percentage of water frozen out at various temperatures by measuring the volume change when ice is formed, by means of a dilatometer. Dieuzeide and Novella (1950) have published a curve for haddock but do not state the method used. Ellis (in preparation, 1956) has worked out a curve for cod muscle based on the freezing of a 1.4% sodium chloride solution which was found isotonic with the muscle from freezing point data. These curves are plotted in Fig. 6. It will be seen that the agreement of the results from these diverse methods is extraordinarily good.

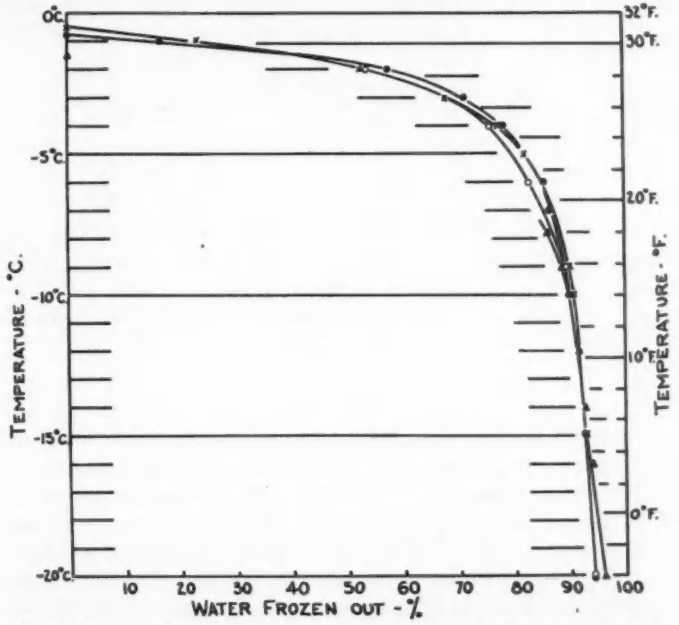

FIG. 6. Amount of water frozen out, as percentage of total water content, at various temperatures.
×—Haddock—Dieuzeide and Novella (1950)
●—Halibut juice—Finn (1934)
△—Lingcod—Mahadevan and Carter (1948)
○—Cod—Ellis (unpublished)

At 0° F., about 93.5% of the water present is frozen out as ice. At 5° F., the 93% frozen out is very little less than at 0° F. However, at 15° F. only 90% is frozen out, which means that 3.5% of the total water melts on transferring frozen fish from 0 to 15° F., and the same amount freezes back into ice on returning the fish to 0° F. From the standpoint of the water remaining unfrozen as brine in the fish, there is 10% as brine at 15° F. but only 6.5% at 0° F. Thus, about one-third of the remaining water present at 15° F. is frozen out as ice at 0° F. This difference is very significant and will greatly affect the hydration of the protein. But between 0 and 5° F. or from 0 to –5°F. the effect is very much less. Thus, fluctuations at storage temperatures above 5° F. result in freezing and melting of much larger amounts of water. In turn, the resulting dehydration and rehydration of the protein micelles would be greater, presumably leading to greater aggregation and a corresponding decrease in extractability and a parallel loss of palatability. Many complex factors are involved in this denaturation and aggregation process, and the mechanism remains to be elucidated. However, allowing the temperature of the stored frozen fish to fluctuate through even the 10-degree interval between +5 and +15° F. would be expected to result in much greater deterioration of the fish than if a similar fluctuation occurred within the lower 10-degree interval between –5 and +5° F. This appears to agree with the results obtained in the present work.

These results have shown the undesirability of shipping frozen cod under conditions such as prevail in refrigerator cars. It would appear that this is an important factor in the deterioration of the frozen fish at present reaching the market. The information obtained indicates that the effect is even more pronounced than was expected, and consequently every consideration should be given this factor in future refrigerator car design and construction.

There are several questions which are unanswered at present, including the effect of the time of exposure to the higher temperature, effect on fish previously stored at –10° F., effect of freshness of fish and their species. Research is proceeding along these lines.

SUMMARY

The question asked by the railways, does storage at 15° F. for short periods as during refrigerator car transportation affect the quality of frozen fish normally held at 0° F. or below, has been answered in the affirmative. Frozen cod fillets subjected to 2-week storage periods at 15° F. after previous and subsequent storage at 0° F. deteriorated in quality more rapidly than the control held at 0° F. Both protein solubility and taste panel ratings decreased. A second storage period at 15° F. further reduced the subsequent storage quality at 0° F. The deterioration was approximately the same whether the 15° F. treatment was given after storage for 1, 3, or 6 months at 0°F.

These results definitely indicate that shipment in our present refrigerator cars at temperatures near 15° F. is undesirable and efforts should be made to provide lower temperatures.

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Yellow Discoloration and Deterioration in Frozen Lobster Meat[1]

By E. G. Bligh and W. J. Dyer
Fisheries Research Board of Canada
Technological Station, Halifax, N.S.
and
D. C. Horne
Department of Fisheries
Fish Inspection Laboratory, Halifax, N.S.

ABSTRACT

The yellow discoloration which occasionally develops in some Atlantic frozen lobster-meat packs on storage was found to be due to oxidation of the red astacene to a yellow pigment. The discoloration, and the accompanying off-odours and off-flavours, can be minimized by the use of hermetically sealed or vacuum-sealed cans, low storage temperatures, and antioxidants.

INTRODUCTION

Freezing and cold storage of lobster meat have become common practice in the Maritime provinces of Canada and have lessened some of the distribution difficulties encountered in the lobster industry. During the past few years it has been observed that in a portion of the pack the surface of the meat becomes yellow in colour and the meat acquires a seaweedy odour and flavour on frozen storage. In advanced stages this condition renders the product very objectionable.

The present investigation was undertaken to determine the cause of the yellow discoloration and to find a remedy. Some of the work has been summarized in a previous communication from these laboratories (Dyer and Horne, 1953).

PRELIMINARY OBSERVATIONS

In the commercial preparation of frozen lobster meat, live lobsters are cooked for a few minutes, the meat is removed by hand, washed, and packed into cans with added pickle. The product is then cooled in ice, or frozen immediately and placed in frozen storage. The four types of containers in common use are: push-cover cans with open seams, hermetically sealed cans, cans hermetically sealed under vacuum, and cans with transparent window tops of cellophane or pliofilm. The commercial frozen storage conditions of this product in the Maritime provinces were found to be poor. Many plants were refrigerating at 10 to 15° F. (−12.2 to −9.4° C.), or even higher.

In the stored frozen packs it was observed that the yellow colour first appears on the highly pigmented tips of the claws and on a ridge of similar non-striated muscle which runs along the back of the claws. Eventually, the yellow discoloration spreads over the surface of the claw and tail meat. It was peculiar to the pigmented surface and did not extend into the white meat. The

[1]Received for publication December 26, 1956.

J. Fish. Res. Bd. Canada, 14(4), pp. 637–644, 1957.
Printed in Canada.

discoloration was most pronounced in meat packed in containers that provided the least protection against the entry of air, for example, window-top and open-seam cans.

Absorption curves of the pigments extracted with acetone from discoloured lobster claws showed more absorption in the yellow region of the spectrum than those from normal red claws. The astacene extracted from freshly boiled lobster claws could be converted readily from a red to a yellow pigment by treatment with hydrogen peroxide.

A preliminary study of the pigments of the hypodermis of cooked lobster claws was carried out using chromatographic techniques (Strain, 1945). An extract of the hypodermis of yellow claws contained a yellow substance (not carotene) which was not found in a similar extract of fresh claws. This substance showed the same absorption spectrum as the yellow product obtained from astacene by hydrogen peroxide oxidation (Fig. 1). This indicated that in the yellow discoloration of frozen lobster meat an oxidative process is involved whereby astacene is converted to a yellow pigment.

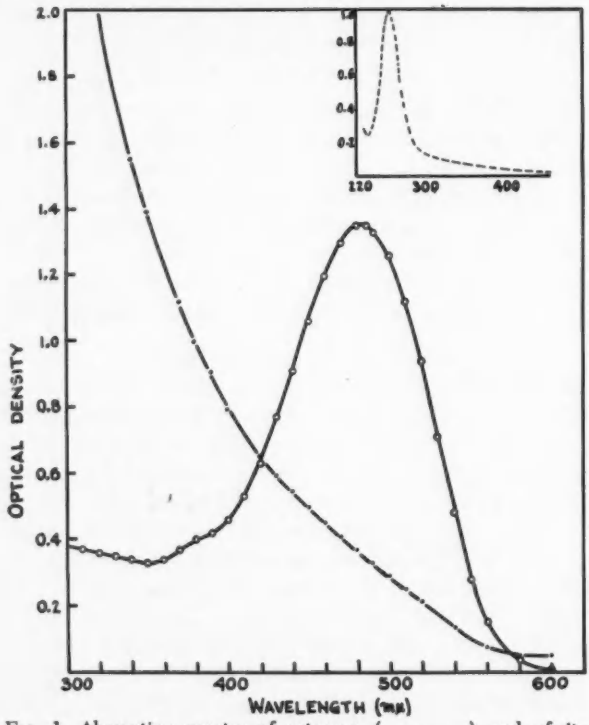

FIG. 1. Absorption spectra of astacene (————) and of its yellow oxidation product (–·–·–) in chloroform. The inset shows the curve obtained for the yellow compound after diluting 500 times with *n*-butanol.

Some earlier reports support the above conclusion and also suggest that fat oxidation may be involved. In 1940, Sumner and Sumner reported that the oxidation of fat and the bleaching of carotene is a coupled reaction. Tarr (1947) stated that rancidity in frozen salmon is accompanied by bleaching of the colour. Reay and House (1951) have reported that low temperature storage of frozen lobsters delayed changes in colour, odour, and taste. Since the completion of the present investigation, Hansen (1955) has confirmed the results of Reay and House and also found that the removal of air proved helpful. In studying the deteriorative changes in frozen shrimp, Faulkner and Watts (1955) suggested that the bleaching of astaxanthin is related to fat oxidation. Dyer *et al.* (1956) found that fading of the red colour of frozen rosefish fillets paralleled fat oxidation and was inhibited by storage at low temperatures and by ascorbic acid.

EXPERIMENTAL

Small market-size lobsters (approximately 1 pound each) caught during the winter season along the south shore of Nova Scotia were used. The live lobsters were steamed for approximately 15 minutes, shucked, and the meat was packed in 6-oz. cans. The pack was rapidly frozen in an air blast freezer and subsequently stored at +10° F (−12.2° C.) or −10° F. (−23.3° C.). The following experimental packs were prepared:

Group A: Stored at +10° F., containing 1 oz. of 8% sodium chloride solution per can.

(1) Control pack—hermetically sealed can.
(2) Window-can pack—window type can (cellophane window).
(3) Oxygen pack—hermetically sealed can, flushed with oxygen gas.
(4) 0.3% Ascorbic acid pack—hermetically sealed can; the salt solution contained 0.3% ascorbic acid.
(5) 1.0% Ascorbic acid pack—hermetically sealed can; the salt solution contained 1.0% ascorbic acid.

Group B: Stored at −10° F., containing 1 oz. of 8% sodium chloride solution per can.

(6) Window-can pack—window type can (cellophane window).

Crude fat was determined on samples of the meat from the tips of the claw, the main part of the claw, and the tail, using the method given by A.O.A.C. (1950).

Every 3 or 4 weeks a sample of each experimental pack of lobster meat was examined. The free fatty acid and peroxide contents of the fat were determined using the methods essentially as described by Dyer and Morton (1956).

For the fat analysis, three or four cans of the frozen lobster meat were allowed to thaw and the meat was separated into tips of claw, main part of claw, and tail meat. After inspection, each portion was broken into small pieces, wrapped in cheesecloth, and most of the pickle was removed by means of a small screw press. The pressed meat (30 to 75 g.), which contained approximately 70% moisture, was mixed with an equal weight of powdered anhydrous sodium

sulphate and 200 ml. of anhydrous chloroform. The mixture was blended for about 30 seconds and filtered through sintered glass. The fat content of the extract was determined by evaporating an aliquot to dryness, under reduced pressure, and weighing the residue.

Since the red colour of the extract masked the end-point in the usual free fatty acid and peroxide value determinations, potentiometric methods had to be employed. A Model G Beckman pH meter was used. A "sleeve type" calomel electrode was found to be more satisfactory than the "fibre type". In the iodometric titration for peroxide a platinum electrode was substituted for the glass electrode. In both determinations stirring was facilitated by a magnetic stirrer.

Free fatty acid was determined by adding 25 to 50 mg. of sodium chloride and 10 ml. of 95% ethanol to 20 ml. of the chloroform extract and titrating potentiometrically with 0.05 N alcoholic sodium hydroxide. Nitrogen was bubbled through the solution during the titration to expel carbon dioxide. The end-point was obtained by plotting $\frac{\Delta(\Delta\ \mathrm{pH})}{\Delta V}$ against the mean volume V. The free fatty acid content was expressed as percentage of extracted fat in terms of oleic acid.

In the determination of peroxide value, 30 ml. of glacial acetic acid and two drops of fresh saturated potassium iodide solution were added to 20 ml. of the extract. After the solution had stood in the dark for 10 min., 50 ml. of distilled water was added and it was titrated potentiometrically with 0.01 N sodium thiosulphate. The volume of thiosulphate was plotted against the e.m.f. and the end point was determined by interpolation. The peroxide value was expressed as milliequivalents (meq.) per 100 g. of fat.

RESULTS AND DISCUSSION

Fat Content

Crude fat determinations on eight cooked lobsters revealed that the meat from the tips of the claw contained more fat than the claw and tail meat. On a wet weight basis the percentage of fat in the tip, claw, and tail meat was 1.6 ($\pm$0.6), 0.9 ($\pm$0.4), and 1.0 ($\pm$0.1), respectively. Thus, considerably more fat is present in that portion of the meat where the yellow colour first develops.

Colour

As previously mentioned, the first colour change occurred on the tips of the claws. No discoloration was observed in the meat from either the main part of the claw or the tail during the periods of frozen storage, but it probably would occur on prolonged storage. The development of off-odours and off-flavours proceeded along with the discoloration and had become pronounced by the time the yellowing became apparent.

The presence of oxygen greatly accelerated the development of the yellow colour. The pack that was flushed with oxygen gas became yellow after storage for 3 weeks at +10° F., whereas the control pack showed no colour change until 10 to 14 weeks of storage. In the window-can pack stored at +10° F. there was a slight discoloration of the claw tips after 11 weeks while the window-can pack

held at –10° F. did not become discoloured until 25 to 28 weeks of storage. There was no discoloration in the meat that was treated with ascorbic acid. The first appearance of yellow colour in the claw tip meat of the various packs is indicated in Fig. 2.

The results show that the presence of oxygen is conducive to yellow discoloration while both low temperature storage and the addition of ascorbic acid inhibit the process.

Texture

Appreciable changes in the texture of the meat did not occur in all the experimental packs. The control pack (+10° F.) and the window-can pack stored at –10° F. showed little change in texture up to 28 weeks of storage, the time at which the experiment was terminated. The window-can pack stored at +10° F., on the other hand, became tough in 14 weeks. It was interesting to note that the presence of oxygen (oxygen pack) had little effect on the texture of the meat, for the storage period used.

As previously mentioned, ascorbic acid prevented the discoloration of frozen lobster meat, but the concentrations used severely affected the texture and taste. The pack containing 1.0% ascorbic acid had become tough and had an acid taste after storage for 3 weeks. The press juice from this pack had a pH of 5.65 (±0.3). The pH of the press juice from the other experimental packs was 7.07 (±0.09). The 0.3% ascorbic acid pack became tough in about 10 weeks and the pH of the press juice was 6.55 (±0.05). It was concluded that the concentrations of ascorbic acid used in the preparation of these packs were much too high.

Free Fatty Acid

During frozen storage there was no significant change in the free fatty acid content of the extracted fat in any of the samples. The average content was 12 to 14%. Hence hydrolysis probably occurred during the preliminary processing of the meat.

Peroxide Value

The change on storage in the peroxide value of the claw tip meat from the various experimental packs is shown in Fig. 2. The 1.0% ascorbic acid pack is not illustrated since the peroxide values did not exceed 1.0 meq. per 100 g. of fat. The peroxide values for the main part of the claw and the tail meat did not increase above 4 to 5 meq. even on prolonged storage, and consequently are not illustrated.

In the oxygen pack, the peroxide value of the claw tip meat reached a high level (8.7 meq.) in 3 weeks. A similar value was not obtained in the control pack until 14 weeks of storage. Thus, the presence of oxygen enhanced the formation of fat peroxides.

By comparing the curves obtained for the window-can pack (+10° F.) and the control pack (+10° F.), there was no great difference in peroxide values during the earlier weeks of storage (see Fig. 2). Later, however, the values for

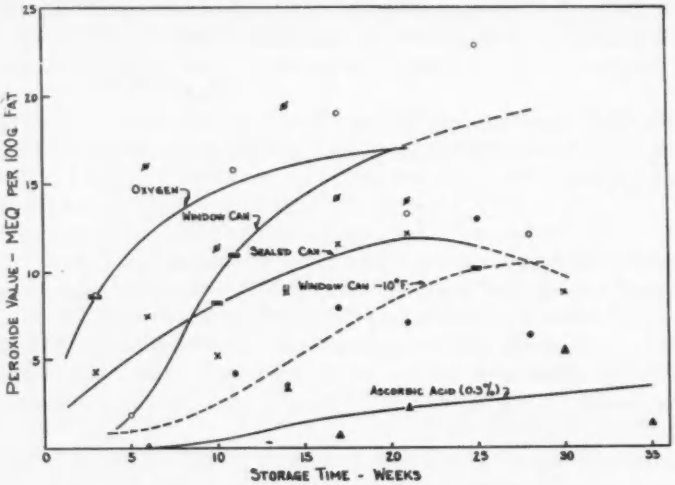

FIG. 2. Peroxide values of claw tip meat on frozen storage.
Stored at +10° F.—Oxygen (Ø), window-can (O), sealed can (×), and 0.3% ascorbic acid (△) packs.
Stored at −10° F.—Window-can (●) pack.
▬ = Appearance of yellow colour.

the control pack were much lower. The difference between effects in these containers was greater in industrial packs where it was observed that the sealed can was superior to the window can.

At +10° F., the peroxide value of the claw tip meat from the window-can pack was 15.8 meq. at 11 weeks, whereas this pack held at −10° F. reached a value of 13.8 meq. only after 25 weeks. Therefore, lowering the storage temperature retarded fat oxidation, a fact already well established (Banks, 1938).

In the 0.3% ascorbic acid pack, the claw tip meat had a peroxide value of 5.5 meq. after storage for 30 weeks at +10° F. Thus, ascorbic acid was effective in inhibiting the formation of fat peroxides.

These investigations have shown that the peroxide value of the fat reaches a relatively high level, 8 to 11 meq., before there is any colour change in the meat. The peroxide value remained at a relatively low level where there was no discoloration, as in the main part of the claw and the tail meat. The claw tip meat which contained the highest concentration of fat and pigment was affected most. On the basis of these findings it was concluded that fat oxidation is the primary reaction, followed by oxidation of the red pigment, probably by the fat peroxides formed.

The off-odours and off-flavours which accompany the yellow colour are at least partly due to rancidity.

The presence of oxygen greatly accelerated the development of the yellow colour, which explains why discoloration was more pronounced in containers

that were not air-tight, such as window-top and open-seam push-cover cans. Furthermore, many of the cellophane windows of the window-top cans become broken under commercial conditions, thus exposing the meat to the air. In this investigation, the window-can pack (+10° F.) did not differ greatly from the sealed-can pack since very few windows were ruptured under laboratory conditions. This is in agreement with the previous finding that cellophane is not a satisfactory packaging material for frozen crab meat (Heerdt and Dassow, 1952).

To prevent the discoloration, air must be excluded from the pack by the use of air-tight containers, such as hermetically sealed cans. The complete removal of air from the pack should prove even more satisfactory. Cans sealed under vacuum are in use in the frozen lobster industry and some tests on an industrial pack have shown that the meat keeps well for at least 6 months. The quality of the product can be maintained even longer if oxidation is inhibited by using a low storage temperature.

Ascorbic acid prevented the yellow discoloration but further work is necessary to determine the optimum concentration which will prevent the colour change and yet will not alter the texture and flavour of the meat. The use of sodium ascorbate, or other antioxidants, might prove more satisfactory. Previous reports have shown that ascorbic acid will inhibit colour changes in salmon (Tarr, 1947), rosefish (Dyer *et al.*, 1956), and shrimp (Faulkner and Watts, 1955).

Recommendations

On the basis of this investigation some recommendations can be made. Cans that allow dehydration or the entry of air, such as window-top and open-seam push-cover cans, should not be used. Hermetically sealed cans, preferably vacuum packed, coupled with quick freezing and low temperature storage (0 to –10° F.) should be used. The addition of an antioxidant, such as ascorbic acid or sodium ascorbate, may also be beneficial.

SUMMARY

It was concluded that the yellow discoloration of frozen lobster meat is due to oxidation of red astacene to a yellow pigment. The presence of oxygen greatly accelerated the development of the yellow colour. In the stored meat, the peroxide value of the fat reached a high level before any discoloration appeared. The discoloration was greatest in the claw tip meat which contained the highest concentration of fat. It was considered that fat peroxides were probably responsible for oxidizing the red pigment. The process can be minimized by protecting the meat from air, packing in hermetically sealed or vacuum-sealed cans, and using low storage temperatures (0 to –10° F.). The use of an antioxidant, such as ascorbic acid or sodium ascorbate, may be helpful.

ACKNOWLEDGMENT

Acknowledgment is made to R. J. McNeill, Department of Fisheries Fish Inspection Laboratory, for aid in the preparation of the experimental packs, to

Margaret L. Morton and R. L. Doyle of the same Laboratory, for technical assistance, and to P. L. Hoogland of the Fisheries Research Board Technological Station for the chromatographic fractionation and identification of the pigments.

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Alterations in the Blood Level of Lactic Acid in Certain Salmonoid Fishes Following Muscular Activity. II. Lake Trout, *Salvelinus namaycush*[1,2,3]

By Edgar C. Black
The University of British Columbia, Vancouver, B.C.

ABSTRACT

During the summer of 1954, 1½-year-old, hatchery-raised lake trout, *Salvelinus namaycush*, were subjected to 15 minutes of severe muscular exercise at the trout hatchery at Summerland, B.C. Following exercise, fish were allowed to recover for various intervals up to 24 hours. Blood samples were taken and analyzed. The hemoglobin levels did not change significantly, the blood glucose increased significantly during the second hour of recovery. Except for dips at the 6th and 12th hours, this high level of glucose persisted to the end of 24 hours. The blood level of lactic acid increased sevenfold immediately following exercise and continued to increase during the first two hours of recovery. The lactic acid level declined rapidly between the 2nd and 6th hour. The initial low unexercised level was reached by the end of 24 hours. The hemoglobin and lactic acid changes were very similar to those noted for Kamloops trout, *Salmo gairdneri*.

INTRODUCTION

Changes in the blood level of lactic acid as a result of muscular activity were observed first in fishes by Secondat and Diaz (1942). These changes were found to be much the same as in mammals, except that the blood lactic acid continued to increase for a longer period of time following activity. There was also a much longer period for the removal of lactic acid. Indeed in some fish, the lactic acid did not diminish, and these fish died a few hours later. Black (1957) has also reported on alterations in lactic acid and blood glucose following severe muscular activity. The changes in lactic acid were much greater in the Kamloops trout, *Salmo gairdneri* (Black, 1957) than in the tench, *Tinca tinca* (Secondat and Diaz, 1942). The blood glucose level in Kamloops trout, *Salmo gairdneri*, increased significantly between the 4th and 8th hour of recovery during which interval the lactic acid level declined. The present paper deals with changes in the blood levels of lactic acid and glucose in the lake trout, *Salvelinus namaycush*, following severe muscular activity.

METHODS

The lake trout were hatched and reared at the Summerland trout hatchery which is operated at Summerland, B.C., by the British Columbia Game Commission. The water supply is of artesian origin. The water is moderately hard and

[1]Received for publication December 24, 1956.
[2]Contribution from the Department of Physiology, Faculty of Medicine, The University of British Columbia; and The British Columbia Game Commission; both at Vancouver, B.C.
[3]This project was supported by The National Research Council of Canada.

J. Fish. Res. Bd. Canada, 14(4), pp. 645–649, 1957.
Printed in Canada.

contains calcium bicarbonate and the temperature ranges from 11.5–12.0° C. the year round. The fish were 1½ years old when used.

The methods used to exercise the fish and to take and analyze the blood have been described in earlier papers (Black, 1955; 1957). Blood samples were taken by cardiac puncture while fish respired in water. A Klett photocolorimeter was used to determine hemoglobin as acid hematin and to determine lactic acid by the Barker-Summerson method (Hawk *et al.*, 1949). Glucose was analyzed by the method of Somogyi (1945). Tungstic acid filtrates were used for the lactic acid determinations, while barium and zinc hydroxide filtrates were used for the glucose estimations.

RESULTS AND DISCUSSION

The results are summarized in Table I and illustrated in the accompanying Figure.

The hemoglobin levels did not change significantly following exercise or during the recovery period from the initial unexercised level.

The lactic acid in the unexercised condition was 13.7 ± 5.3 mg.% (mg. per 100 ml. of whole blood). This may be compared with an average of 8.0 ± 0.9 mg.% for two-year-old Kamloops trout and 15.7 ± 1.1 mg.% for yearling Kamloops trout (Black, 1957).

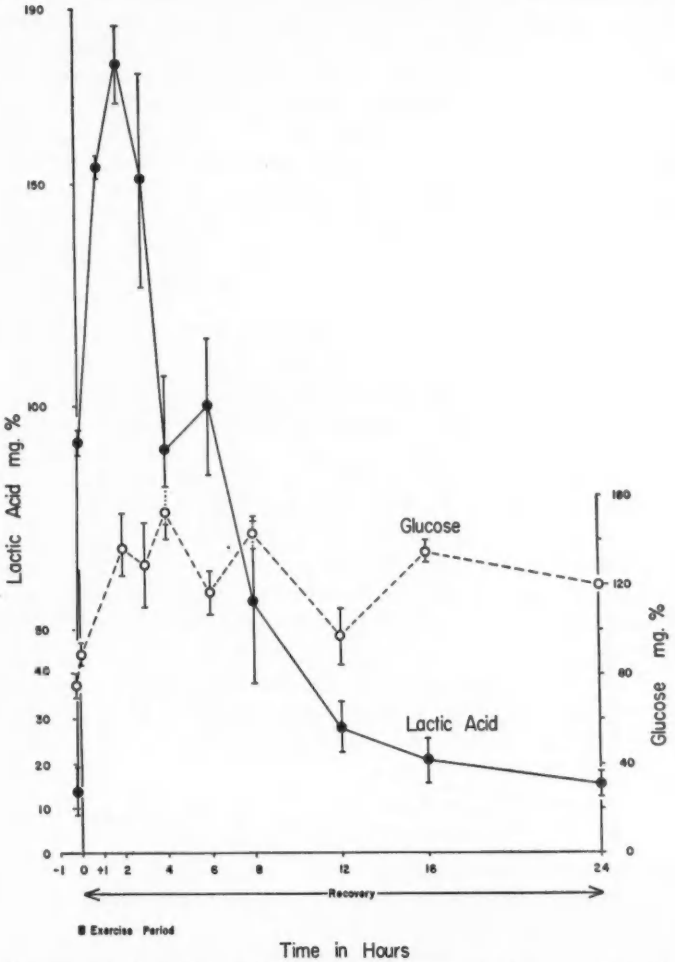
TABLE I. Average weights and average levels of hemoglobin, glucose, and lactic acid in the blood of 1½-year-old lake trout following 15 minutes of muscular exercise and recovery therefrom. Temperature 11.5°C. The standard error of the average is given after the average. The number of determinations is given in parentheses below the average.

Condition	Average weight	Average hemoglobin	Average blood glucose	Average blood lactic acid
	g.	*g.%*	*mg.%*	*mg.%*
Unexercised	132 ± 5.7 (13)	9.6 ± 0.29 (13)	74.7 ± 5.27 (10)	13.7 ± 5.27 (13)
Exercised 15 minutes	116 ± 7.3 (16)	9.3 ± 0.36 (16)	87.6 ± 6.11 (10)	91.9 ± 2.73 (16)
Recovered 1 hour	76 (3)	10.5 (3)	—	154 ± 1.93 (3)
Recovered 2 hours	121 ± 7.1 (11)	10.6 ± 0.43 (11)	136 ± 11.9 (6)	177 ± 9.04 (11)
Recovered 3 hours	144 ± 16.6 (9)	10.5 ± 0.47 (8)	128 ± 18.4 (8)	151 ± 24.2 (8)
Recovered 4 hours	137 ± 6.8 (10)	10.6 ± 0.23 (8)	152 ± 11.7 (7)	90.0 ± 16.7 (10)
Recovered 6 hours	125 ± 8.8 (8)	9.7 ± 0.35 (8)	116 ± 10.1 (3)	99.9 ± 15.4 (8)
Recovered 8 hours	130 ± 14.7 (6)	10.0 ± 0.47 (6)	143 ± 6.5 (4)	56.0 ± 18.2 (6)
Recovered 12 hours	122 ± 9.9 (10)	9.1 ± 0.23 (9)	96.6 ± 13 (7)	27.9 ± 5.5 (10)
Recovered 16 hours	120 ± 17.0 (5)	9.9 ± 0.45 (5)	134 ± 4.4 (5)	21.0 ± 5.5 (5)
Recovered 24 hours	98.8 ± 9.9 (6)	9.4 ± 0.58 (6)	120 ± 0.5 (2)	15.3 ± 2.7 (6)

Immediately following 15 minutes of severe and continuous exercise, the lactic acid of the blood of lake trout increased to 91.9 ± 2.7 mg.%. This may be compared with a value of 82.2 ± 10.0 mg.% for two-year-old Kamloops trout,

99.8 ± 1.0 mg.% for yearling Kamloops trout (Black, 1957). Accordingly, there was a 7-fold increase in the lactic acid in blood immediately following the severe exercise. The change was of the same order as that observed for the Kamloops trout.

During the recovery period, the blood level of lactic acid in the lake trout increased to 177 ± 9.0 mg.%, after 2 hours. From the 2nd to 4th hour of recovery,



Alterations in the blood levels of lactic acid and glucose in one-and-a-half-year-old lake trout following severe exercise for 15 minutes and recovery therefrom at 11.5° C. The averages for the lactic acid are shown as solid circles; glucose, open circles. The distance between the vertical bars represents twice the standard error of the average.

the lactic acid declined precipitously to 90.0 ± 16.7 mg.%. The decline continued between the 6th and 12th hour to a level of 27.9 ± 5.5 mg.%. At the end of 24 hours of recovery, the lactic acid in the blood was 15.3 ± 2.7 mg.%, or approximately the same as the initial level (see accompanying Figure).

These changes follow very closely the changes reported for the two-year-old Kamloops trout (Black, 1957).

The explanation for the alterations in the blood levels for lactic acid are the same for the two species of fish. Presumably, muscle glycogen is hydrolyzed during the severe activity finally to lactic acid. It is also presumed that the lactic acid diffuses from the muscles slowly due to the effect of lowered temperature upon diffusion (Johnson *et al.*, 1945). Ultimately, the lactic acid is removed from the blood.

The blood glucose level for the unexercised lake trout was 74.7 ± 5.3 mg.%. Lang and Macleod (1920) obtained 81 mg.% for the lake trout. The value for the unexercised Kamloops trout is lower, 60 ± 6 mg.% (Black, 1957). Kiermeier (1939) found that the blood glucose in the rainbow trout, *Trutta iridea* = *Salmo gairdneri*, was 71 mg.% using the chemical method and 48 mg.% using a fermentation method of analysis.

In the lake trout, the blood glucose level did not increase significantly immediately after exercise (Table I, Figure). However, readings taken at the end of 2 hours of recovery were significantly higher than the blood glucose level immediately after exercise. The increase persisted at a high level through to the end of 24 hours except for a drop to 96 mg.% at the 12-hour period. This response in blood glucose following activity appeared earlier and persisted longer in the lake trout than in the Kamloops trout. In Kamloops trout blood glucose did not increase significantly till the 8th hour at which time the lactic acid decreased significantly; the blood glucose declined at the end of 24 hours toward the initial unexercised level. It will be interesting to determine what relationship, if any, the increased blood level of glucose in the lake trout following activity may have to the possible restoration of muscle glycogen.

Scott (1921) found that removing the dog fish, *Mustelis canis* from water for 80 seconds increases the blood sugar from 70 to 170 mg.% in 2½ min. Simpson (1926) and Menten (1927) also observed increases in blood sugar of fish following exposure to air.

SUMMARY

1. Immediately following severe muscular activity for 15 minutes, the blood levels of hemoglobin and glucose were not altered significantly, but the level of lactic acid increased sevenfold.

2. During the recovery period, up to 24 hours, there was no significant change in the hemoglobin level.

3. The blood glucose level increased significantly at the 2nd hour and persisted at this level to the end of 24 hours except for dips at the 6th and 12th hours.

4. The lactic acid level continued to increase during the first 2 hours of recovery immediately following exercise. After the 2 hours of recovery, the lactic acid level declined precipitously for the next 2 hours. By the 24th hour, the level had dropped to the initial unexercised value.

5. On the whole, the changes in blood lactic acid and glucose are the same as changes reported for the Kamloops trout.

ACKNOWLEDGMENTS

The author is greatly indebted to the National Research Council of Canada for a grant-in-aid supporting this project. Messrs. F. D. Forbes and A. J. Macgregor acted as technical assistants. The generous help of Messrs I. Barrett and D. Hurn of the British Columbia Game Commission is also acknowledged.

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Possible Effects of Water Diversions on Fish Distribution in British Columbia[1]

By C. C. Lindsey

British Columbia Game Commission, and
Institute of Fisheries, University of British Columbia
Vancouver, B.C.

ABSTRACT

The known distributions of freshwater fishes in drainages of the British Columbia mainland are summarized, including those of five species not previously recorded from the province. The continental divide forms a break in fish distribution; 35 of the 57 species on the Pacific slope in B.C. do not occur in the Mackenzie or Yukon River drainages of the province, and 11 of the 33 species in the latter area occur nowhere on the Pacific slope. Some proposed water diversions for hydroelectric development would cross the continental divide, and are likely to produce striking changes in fish distribution. A proposed Liard-Stikine diversion would probably introduce several species, including trout, into the upper Liard River, and several other species, including northern pike (*Esox lucius*) into the Stikine River. A proposed Peace-Fraser diversion would introduce into the Fraser River arctic grayling, and possibly several other species including northern pike. Other proposed diversions are discussed, and their probable affects on fish distribution are listed. Any diversion introducing pike into waters supporting Pacific salmon (*Oncorhynchus*) is liable to be economically harmful, as pike are voracious fish-eaters. Pike are also vectors of *Triaenophorus* tape-worm, which has been found in Alaska to encyst in the flesh of Pacific salmon in a watershed inhabited by pike.

INTRODUCTION

In British Columbia several sites exist for the development of large blocks of hydroelectric power through the diversion towards the coast of headwaters of interior drainages. One such site has already been developed near Kitimat, and several others are under active study. So far, waters in British Columbia have been diverted only between different Pacific slope river systems, but some schemes now under discussion involve directing waters across the continental divide, from either the Arctic Ocean drainage (Mackenzie River headwaters) or the Bering Sea drainage (Yukon River headwaters) into watersheds of the Pacific.

When rivers are diverted into new courses, fish may be carried over into areas from which they were formerly excluded. Because the fish faunas of adjacent north Pacific river systems do not differ markedly, artificial diversions completed to date probably have not produced marked changes in fish distribution. If, however, rivers from beyond the continental divide are diverted onto the Pacific slope, more striking changes in fish distribution are likely to result, with possible economic consequences.

This paper summarizes present distribution patterns of all fishes known from the British Columbia mainland, and discusses some alterations which may be

[1]Received for publication February 4, 1957.

J. Fish. Res. Bd. Canada, 14(4), pp. 651–668, 1957.
Printed in Canada.

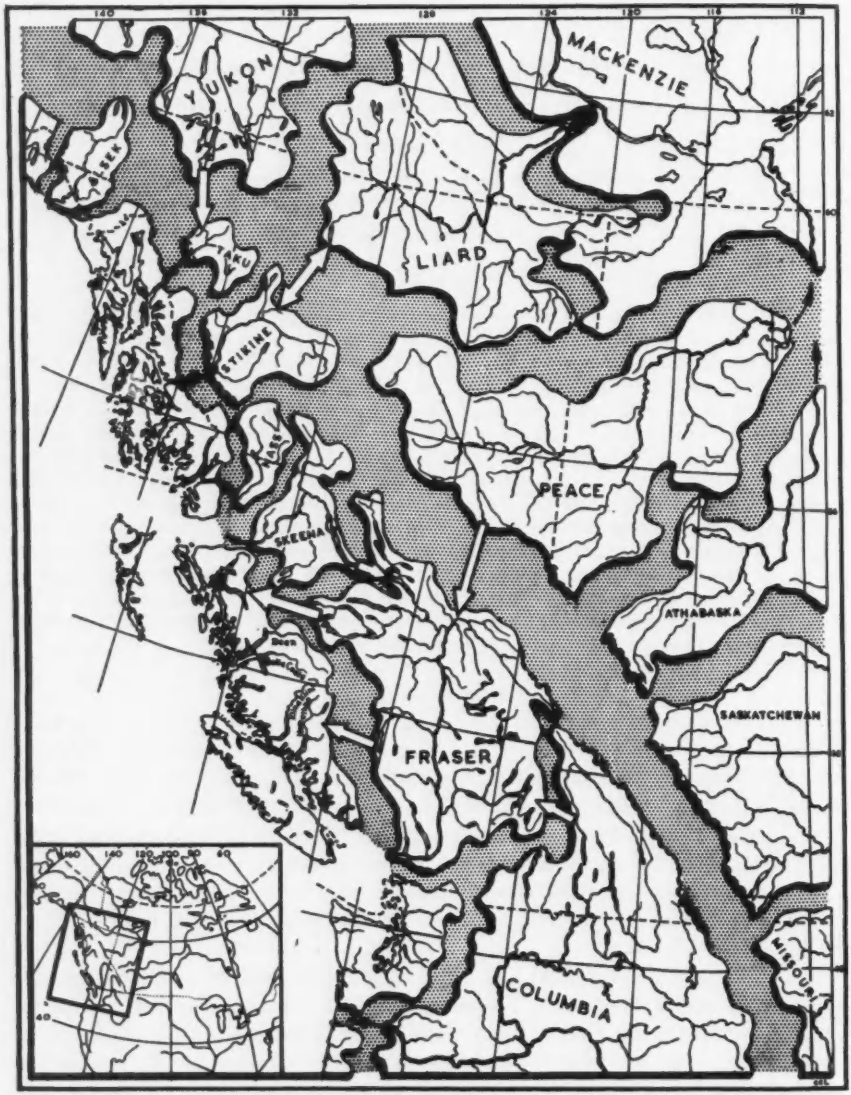

FIG. 1. Disarticulated map, showing watersheds as parts of a "jig-saw puzzle" which have been moved apart to expose a stippled area beneath. White arrows indicate water diversions discussed in text.

produced by certain proposed hydroelectric diversions. Only those alterations resulting from introduction of fish are dealt with; the direct effects of dams, such as obstruction of spawning runs, are beyond the scope of this discussion.

Statements of distributions are based on published records, and on recent collections made largely by personnel of the British Columbia Game Commission and deposited in the Institute of Fisheries at the University of British Columbia. New distribution records relating to the discussion are listed in the Appendix, which summarizes all records for British Columbia mainland drainages.

PRESENT FISH DISTRIBUTION

Drainage systems and watershed boundaries in British Columbia are shown in Fig. 1. Major rivers on the Pacific slope are, from south to north, the Columbia, Fraser, Skeena, Nass, Stikine and Taku. The Alsek River watershed crosses the extreme northwestern tip of the province, but shares no boundary with the Taku. All the other rivers named share watershed boundaries with their listed neighbours, and all but the Nass extend inland to the continental divide. Between the Skeena and Fraser River mouths is a series of shorter coastal rivers.

The upper Columbia River system in British Columbia is separated by the ridge of the Rocky Mountains from the Saskatchewan and Athabaska River headwaters in Alberta. The Fraser headwaters border those of the Athabaska and Peace, while the Skeena borders only the Peace River section of the Mackenzie drainage. The Stikine is adjacent to the Peace and Liard River headwaters, and also, to the north, the headwaters of the Yukon River. The Taku also borders the Yukon system.

Table I summarizes the known distribution of freshwater fishes in principal drainages of the British Columbia mainland, and gives their scientific names. Reasons for certain changes in the common or scientific names used by Carl and Clemens (1953) have been given previously (Lindsey 1956a, b). Five species listed in Table I have not been recorded previously from the province; data on these are included in the Appendix.

The barrier of the continental divide forms a distinct faunal break in the fish distributions shown. Thirty-five of the 57 species on the Pacific slope in British Columbia do not occur in the Mackenzie or Yukon River drainages of the province, and eleven of the 33 species in the latter areas occur nowhere on the Pacific slope. The same contrast does not exist between faunas of adjoining river systems *within* the Pacific slope, although there is a progressive decrease towards the north in the number of species per river. Eighteen species occur in all major river systems from the Columbia (including its lower portions in Washington) north to the Taku. Most other Pacific slope species evidently originated south of the ice sheet and have since extended northward from the Columbia system for varying distances up the coast. (As examples, peamouth, redside shiners and largescale suckers range north to the Nass, while squawfish range only as far north as the Skeena). Exceptions are formed to the usual pattern by the breakthrough of some Mackenzie and Yukon forms into northern coastal drainages; the occurrence of arctic grayling and round whitefish in the Alsek River, of grayling

TABLE I. Distribution of fishes in river systems of British Columbia mainland.
Reference letters are as follows: A—see Appendix; C—Carl and Clemens, 1953; L—Lindsey, 1956b; ?—occurrence surmised from known limits of distribution.

Species No.	Common and scientific name	Columbia R. in B.C.	Fraser R.	Coast drainages south of Skeena R.	Skeena R.	Nass R.	Stikine R.	Taku R.	Yukon R. in B.C.	Liard R. in B.C.	Peace R. in B.C.
1	Southern grayling *Thymallus arcticus tricolor* (Cope)	A	.	.	.	.	.	.	.	.	.
2	Northern mountain-sucker *Pantosteus jordani* Evermann	A	.	.	.	.	.	.	.	.	
3	Tench *Tinca tinca* (Linnaeus)	C	.	.	.	.	.	.	.	.	.
4	Speckled dace *Rhinichthys osculus* (Girard)	A	.	.	.	.	.	.	.	.	.
5	Black bullhead *Ictalurus melas melas* (Rafinesque)	C	.	.	.	.	.	.	.	.	.
6	Yellow perch *Perca flavescens* (Mitchill)	C	.	.	.	.	.	.	.	.	.
7	Smallmouth bass *Micropterus dolomieui* Lacépède	C	.	.	.	.	.	.	.	.	.
8	Largemouth bass *Micropterus salmoides* (Lacépède)	C	.	.	.	.	.	.	.	.	.
9	Pumpkinseed *Lepomis gibbosus* (Linnaeus)	C	.	.	.	.	.	.	.	.	.
10	Columbia sculpin *Cottus hubbsi* Bailey and Dimick	A	.	.	.	.	.	.	.	.	.
11	Torrent sculpin *Cottus rhotheus* (Rosa Smith)	C	.	.	.	.	.	.	.	.	.
12	Shorthead sculpin *Cottus* sp.	A	.	.	.	.	.	.	.	.	.
13	Yellowstone cutthroat trout *Salmo clarki lewisi* (Girard)	C	C	.	.	.	.	.	.	.	.
14	Eastern brook trout *Salvelinus fontinalis* (Mitchill)	C	C	.	.	.	.	.	.	.	.
15	Bridgelip sucker *Catostomus columbianus* (Eigenmann and Eigenmann)	L	L	.	.	.	.	.	.	.	.

16	Carp *Cyprinus carpio* Linnaeus	C	C	.	.	.	.	.	.	.	.
17	Chiselmouth *Acrocheilus alutaceum* Agassiz and Pickering	C	A	.	.	.	.	.	.	.	.
18	Leopard dace *Rhinichthys falcatus* (Eigenmann and Eigenmann)	C	C	.	.	.	.	.	.	.	.
19	Western brook lamprey *Lampetra planeri* (Bloch)	.	C	.	.	.	.	.	.	.	.
20	River lamprey *Lampetra fluviatilis* (Linnaeus)	.	C	.	.	.	.	.	.	.	.
21	Goldfish *Carassius auratus* (Linnaeus)	.	C	.	.	.	.	.	.	.	.
22	Brown bullhead *Ictalurus nebulosus nebulosus* (LeSueur)	.	C	.	.	.	.	.	.	.	.
23	Black crappie *Pomoxis nigromaculatus* (LeSueur)	.	C	.	.	.	.	.	.	.	.
24	Green sturgeon *Acipenser medirostris* Ayres	.	C	.	.	.	.	.	.	.	.
25	Pacific lamprey *Entosphenus tridentatus* (Gairdner)	C	C	?	C	?	?	?	.	.	.
26	American shad *Alosa sapidissima* (Wilson)	.	C	?	?	?	?	?	.	.	.
27	Eulachon *Thaleichthys pacificus* (Richardson)	.	C	?	C	C	?	?	.	.	.
28	Aleutian sculpin *Cottus aleuticus* Gilbert	.	C	A	C	?	A	?	,	.	.
29	White sturgeon *Acipenser transmontanus* Richardson	.	C	?	?	?	?	A	.	.	.
30	Coastal cutthroat trout *Salmo clarki clarki* Richardson	.	C	A	A	A	A	A	.	.	.
31	Threespine stickleback *Gasterosteus aculeatus* Linnaeus	.	C	A	A	?	?	A	.	.	.
32	Longfin smelt *Spirinchus dilatus* Schultz and Chapman	.	C	?	?	?	?	A	.	.	.
33	Pink salmon *Oncorhynchus gorbuscha* (Walbaum)	.	C	A	C	C	A	A	.	.	.
34	Coho salmon *Oncorhynchus kisutch* (Walbaum)	.	C	A	C	C	A	A	.	.	.
35	Sockeye salmon and kokanee *Oncorhynchus nerka* (Walbaum)	C	C	A	A	A	C	A	.	.	.
36	Chinook salmon *Oncorhynchys tshawytscha* (Walbaum)	.	C	A	C	A	A	A	C	.	.

TABLE I.—continued.

Species No.	Common and scientific name	Columbia R. in B.C.	Fraser R.	Coast drainages south of Skeena	Skeena R.	Nass R.	Stikine R.	Taku R.	Yukon R. in B.C.	Liard R. in B.C.	Peace R. in B.C.
37	Chum salmon *Oncorhynchus keta* (Walbaum)	.	C	C	C	C	C	A	C	.	.
38	Lake whitefish *Coregonus clupeaformis* (Mitchill)	C	C	.	A	.	.	.	C	L	L
39	Burbot *Lota lota* (Linnaeus)	C	C	.	A	.	.	.	C	L	L
40	Slimy sculpin *Cottus cognatus* Richardson	C	L	.	.	.	A	.	C	L	L
41	Longnose sucker *Catostomus catostomus* (Forster)	C	C	A	A	A	A	?	C	L	L
42	Lake trout *Salvelinus namaycush* (Walbaum)	.	C	.	A	.	A	A	C	L	L
43	Arctic grayling *Thymallus arcticus signifer* (Richardson)	.	.	.	.	.	A	A	C	L	L
44	Northern pike *Esox lucius* Linnaeus	.	.	.	.	.	.	A	C	L	L
45	Dolly Varden *Salvelinus alpinus malma* (Walbaum)	C	C	A	A	A	A	A	.	L	L
46	Lake chub *Couesius plumbeus* (Agassiz)	C	C	.	A	.	A	.	L	L	L
47	Pygmy whitefish *Coregonus coulteri* Eigenmann and Eigenmann	C	L	.	L	.	.	.	.	L	.
48	Longnose dace *Rhinichthys cataractae* (Valenciennes)	C	C	A	A	.	.	.	.	L	L
49	White sucker *Catostomus commersoni* (Lacépède)	.	L	.	A	.	.	.	.	L	L
50	Mountain whitefish *Coregonus williamsoni* Girard	C	C	A	A	A	A	A	.	L	L
51	Brassy minnow *Hybognathus hankinsoni* Hubbs	.	C	.	.	.	.	.	.	.	L
52	Northern squawfish *Ptychocheilus oregonense* (Richardson)	C	C	A	A	.	.	.	.	.	L

53	Largescale sucker *Catostomus macrocheilus* Girard	C	C	A	A	A	.	.	.	.	L
54	Peamouth *Mylocheilus caurinum* (Richardson)	C	C	A	A	A	.	.	.	.	L
55	Redside shiner *Richardsonius balteatus* (Richardson)	C	C	A	A	A	.	.	.	.	L
56	Prickly sculpin *Cottus asper* Richardson	C	C	A	A	A	A	?	.	.	L
57	Steelhead and rainbow trout *Salmo gairdneri* Richardson	C	C	A	A	A	A	A	.	.	L
58	Broad whitefish *Coregonus nasus* (Pallas)	.	.	.	.	.	.	.	C	.	.
59	Least cisco *Coregonus sardinella* Valenciennes	.	.	.	.	.	.	.	C	.	.
60	Inconnu *Stenodus leucichthys nelma* (Pallas)	.	.	.	.	.	.	.	C	.	.
61	Round whitefish *Coregonus cylindraceus* Pallas	.	.	.	.	.	.	.	C	L	.
62	Flathead chub *Platygobio gracilis* (Richardson)	.	.	.	.	.	.	.	.	L	L
63	Trout-perch *Percopsis omiscomaycus* (Walbaum)	.	.	.	.	.	.	.	.	L	L
64	Yellow walleye *Stizostedion vitreum vitreum* (Mitchill)	.	.	.	.	.	.	.	.	L	L
65	Spoonhead sculpin *Cottus ricei* Nelson	.	.	.	.	.	.	.	.	L	L
66	Northern pearl dace *Margariscus margarita nachtriebi* (Cox)	.	.	.	.	.	.	.	.	.	L
67	Northern redbelly dace *Chrosomus eos* Cope	.	.	.	.	.	.	.	.	.	L
68	Brook stickleback *Eucalia inconstans* (Kirtland)	.	.	.	.	.	.	.	.	.	L

and northern pike in the Taku River, and of grayling and possibly of the slimy sculpin in the Stikine River, are all attributable to headwater capture.

The distributions of some economically significant species are sharply delimited by watershed boundaries. Five species of Pacific salmon occur in all the coastal drainages but are absent from the entire Mackenzie system within British Columbia. Two of these species, the chinook (spring) and chum salmon, also ascend the Yukon River to its headwaters in northwestern British Columbia. Cutthroat and rainbow or steelhead trout occupy all the west slope drainages. Rainbow trout are present in the Peace system, but trout (as distinct from char) evidently do not occur in the Liard or the British Columbia portion of the Yukon system.

Distribution of the northern pike approximately complements that of the Pacific salmon. Pike occupy the Yukon and Liard systems, and have been taken from the Peace River as far upstream as Hudson Hope (see Fig. 2). On the Pacific slope the species is apparently limited to the headwaters of the Taku.

The northern squawfish is a large piscivorous minnow indigenous to the

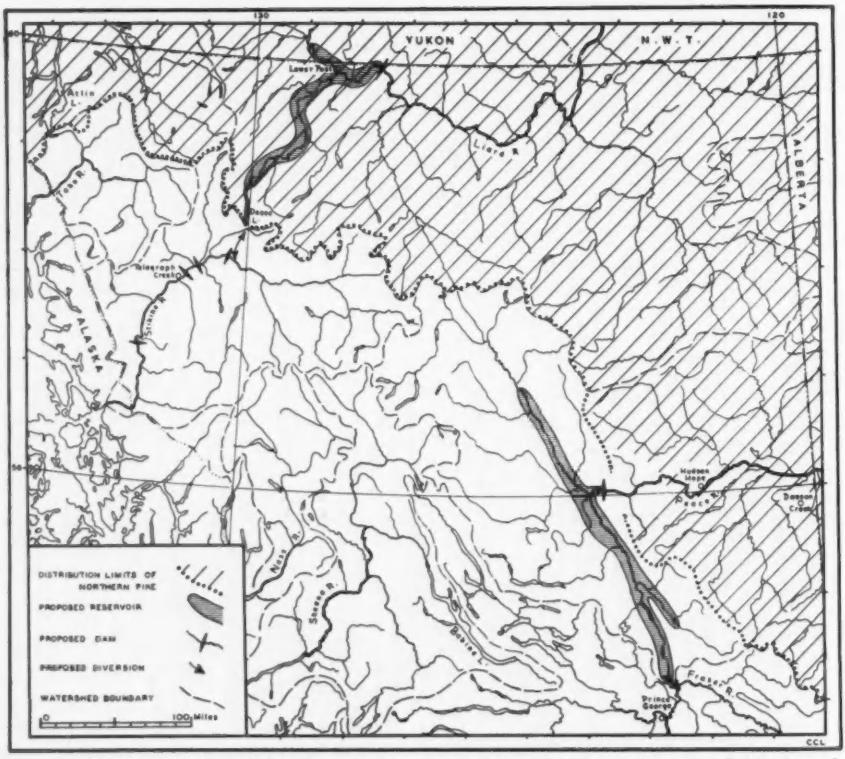

FIG. 2. Northern British Columbia, showing approximate location of proposed Liard and Peace River reservoirs (after Smith, 1955), and probable distributional limits of northern pike.

west slope, extending into the Mackenzie system only in the upper Peace (to which it and several other species have probably gained entry only in comparatively recent time (Lindsey, 1956b)). Squawfish are apparently absent from Pacific drainages north of the Skeena. Thus the Nass and Stikine drainages currently lack both pike and squawfish.

The arctic grayling is a fish of increasing recreational value which occupies the Peace, Liard and Yukon systems, and, on the west coast, the Taku, Stikine and Alsek. It is absent from more southerly west coast drainages, although a closely related and perhaps identical form, the southern grayling, occurs as a relict in the upper Columbia and Missouri systems and enters British Columbia in the Flathead River (and has recently been planted in the Kootenay district outside its natural range).

PROPOSED LIARD-STIKINE DIVERSION

A plan to develop hydroelectric power at sites along the Stikine River has been outlined by Smith (1955). In order to compensate for rapid fluctuation in flow of the Stikine, the upper Liard would be dammed a few miles below Lower Post. This would create a reservoir extending up the Dease River to Dease Lake, which would be connected by canals or tunnels to the Stikine system (Fig. 2). Surplus water from the Stikine could be transferred to the Liard reservoir and returned along with Liard water to create power as desired at sites on the Stikine. This two-way exchange of water would virtually ensure the interchange of species now found in the headwaters involved. Appreciable changes in the fauna would result, for of the 33 species listed for the Stikine or Liard, only 7 occur in both systems.

The northern pike would very probably enter the Stikine from the Liard were this plan implemented, for pike are now abundant in Dease Lake (Fig. 2). There is the further possibility that, once they occupied the Stikine basin, pike would subsequently spread southward at certain low points into the Nass or Skeena basins. As pike are voracious fish-eaters, they might make appreciable inroads into populations of young Pacific salmon. The impact of pike on the salmon fisheries of the Stikine and Nass rivers might be strengthened by the fact that salmon of these systems do not now have to contend either with pike or with squawfish (which are also piscivorous).

In addition to its direct effect as a predator, the pike would probably serve as vector of a parasite new to the Pacific slope. The tape-worm *Triaenophorus crassus* Forel utilizes the northern pike as its definitive host (Miller, 1952). Although this parasite does not infect man, it does form cysts in the muscles of other species of fish which are intermediate hosts, rendering their flesh unattractive and unmarketable. *Triaenophorus* infestation has been of major economic concern in many North American lakes supporting commercial fisheries. Species infested as intermediate hosts include whitefish, arctic grayling and, in Europe, three species of salmonids. The parasite already occurs in fishes of the Mackenzie drainage in British Columbia, as it has been found in lake whitefish from Moberley Lake (which also contains pike) 60 miles west of Dawson Creek

(J. R. Adams, personal communication), as well as in Teslin Lake on the Yukon River system (Clemens, Boughton and Rattenbury, 1945). That *Triaenophorus* would spread to Pacific salmon in any Pacific slope drainage to which pike were introduced is suggested by observations in the Bristol Bay area on the Bering Sea. Here both pike and sockeye salmon occupy the Woods River system, and both species harbour *Triaenophorus crassus* (Lawler and Scott, 1954). Of 26 sockeye smolts examined from Lake Aleknagik in this area, 37% contained encysted larvae, while 291 smolts similarly examined from various lakes of the Skeena, Fraser and Columbia contained no *Triaenophorus* (L. Margolis, personal communication). In all areas harbouring this species of tape-worm, presence of pike (or of muskellunge) is the common denominator.

Four other species have been taken from the Liard River upstream of Lower Post and would therefore be carried over into the Stikine system. These are the round whitefish, pygmy whitefish, lake whitefish and longnose dace. Other species known to occur farther down the Liard and which might gain entry to the Stikine are the white suckers, flathead chub, burbot, trout-perch, yellow walleye and spoonhead sculpin.

Of possible species entering the Liard from the Stikine, the trout are notable. Rainbow trout would almost certainly be transferred by the development outlined, for they now occupy the Tanzilla River, a tributary of the Stikine, within four miles of the south end of Dease Lake. Coastal cutthroat trout have also been taken in the Stikine at Telegraph Creek, and might gain entry into the Mackenzie system. Either species of trout might be expected to establish itself successfully. Whether or not they would spread into the lower reaches of the Liard would depend on whether or not water were allowed to escape through the Liard dam.

All five species of Pacific salmon spawn in the Stikine, but are not likely to have the opportunity to establish themselves in the Liard. (Chum, sockeye and pink are reported from the lower Mackenzie River, and chum have been taken between Lake Athabaska and Great Slave Lake.) The prickly sculpin occurs in the headwaters of the Stikine and would probably be introduced to the Liard. Seven other species listed from the Stikine but not the Liard are usually absent from headwaters and therefore might not be involved in the proposed diversion.

Seven more species are already found in both systems, including the arctic grayling and slimy sculpin. The latter has, like the grayling, probably invaded the Stikine through headwater capture, for the only other area where it is known to occur close to the Pacific Ocean is in drainages in the vicinity of Cook Inlet in Alaska. It is absent from the Skeena, and has been taken from the Fraser only in the upper reaches above Quesnel, and from the Columbia only in the northern headwaters.

The probable effect of the proposed Liard-Stikine diversion on fish distribution would be to introduce several species, including trout, into the upper Liard, and several species, including northern pike, into the Stikine. Pacific salmon in the Stikine might be adversely affected by pike, and might become infested with *Triaenophorus* tape-worm.

PROPOSED YUKON-TAKU DIVERSION

The proposal to develop power by diversion of a portion of the headwaters of the Yukon River into the valley of the Taku River (Withler, 1956) is sometimes known as the "Frobisher Scheme". This project, involving one-way diversion of water, would allow the transfer of fish from the Yukon to the Taku River, but not from the Taku to the Yukon.

Eight species which occur in the Yukon headwaters in British Columbia have not been reported from the Taku (although some may be disclosed by more extensive collection). These are the round whitefish, lake whitefish, broad whitefish, least cisco, inconnu, lake chub, burbot and slimy sculpin. Of these, the inconnu and burbot are piscivores which might make some inroads into stocks of fish native to the Taku. Inconnu in Great Slave Lake are almost exclusively piscivorous, and are restricted to shallow water (Fuller, 1955).

Six other species are common to the two systems, including arctic grayling and northern pike. Fifteen species are probably found in the Taku but not the upper Yukon, but the nature of the diversion would not furnish these with the opportunity to enter the Yukon system.

Although pike already occupy part of the Taku system, they are so far reported only from the Paddys Lake–Taysen Lake system, which drains by an intermittent stream into the Nakina River. Impassable falls on the Nakina between this point and its entry into the main Taku River block ascent of salmon, so pike and salmon evidently do not come in contact. The proposed diversion from Atlin Lake would introduce water from the Yukon headwaters into the Taku west of the area discussed, and might spread pike (and *Triaenophorus*) more widely through the system.

PROPOSED PEACE-FRASER DIVERSION

This scheme, as outlined by Smith (1955), involves damming of the Peace River where it crosses the Rocky Mountains, in order to create a reservoir along the valleys of the Finlay and Parsnip rivers which would be diverted southward into the Fraser by a canal from Summit Lake (Fig. 2). Power would be developed at Giscombe Rapids above Prince George, and possibly also at points farther down the Fraser. Fish would probably be transferred only in one direction.

Nine species of fish not found in the Fraser River occupy the British Columbia portion of the Peace River. Six of these might be involved in the transfer. Arctic grayling occur in the Finlay and Parsnip systems above the damsite, and would therefore very probably reach the Fraser. Northern pike have been reported as far upstream as Hudson Hope at the lower end of the Peace River canyon (Fig. 2). The area has been little studied, and the precise western limit of their range in the Peace River is unknown. Whether or not they would occupy the reservoir and invade the Fraser system would depend on whether the dam lay above or below the highest point to which they now ascend the Peace. Four other species now absent from the Fraser have also been taken from the Peace only below Hudson Hope, so their inclusion in the proposed reservoir

is problematical. They are yellow walleye (or pike-perch), flathead chub, trout-perch and spoonhead sculpin.

The influence of pike on Pacific salmon in the Fraser is unpredictable, but any effect is likely to be adverse. Moreover, the Fraser system supports a major sport fishery, largely for rainbow trout. Pike, if introduced to the Fraser near Prince George, would gain entry to many lakes supporting sport fishing. Again their effect cannot be clearly forecast, but their arrival would not likely be welcomed by trout fishermen. Similarly, the walleye, which is largely a fish-eater, could make inroads into stocks of trout and salmon. Trout might, like the salmon, also suffer indirectly by infestation with *Triaenophorus*. In partial compensation, the probable introduction of arctic grayling, and the possible introduction of pike and walleye, might themselves establish minor sport fisheries new to the Fraser system.

PROPOSED DIVERSIONS BETWEEN PACIFIC WATERSHEDS

Various diversions of water between Pacific watersheds in British Columbia have been proposed. Because of the similarity in faunas of adjacent river systems on the western slope, described previously, these diversions are not likely to produce important changes in fish distribution. A few such proposals are discussed here briefly.

Skeena-Fraser Diversion

A plan has been proposed to dam the outlet of Babine Lake on the Skeena system, and divert water via a five-mile tunnel into Stuart Lake on the upper Fraser system (Fig. 1). This would be used, in conjunction with water storage in other areas, to develop hydroelectric power at a series of sites along the Fraser (Department of Fisheries *et al.*, 1955). The diversion would not produce many changes in fish distribution, as 29 species are now common to the two systems. No new species could be introduced to the Fraser, as every one known from the Skeena has already been taken in the Fraser. The check-list of Fraser species includes 14 not recorded from the Skeena, but most of these do not occur in the northwestern headwaters. Even if conditions in the diversion allowed fish to move into the Skeena from the Fraser, which is most unlikely, only three species are liable to be involved—bridgelip suckers, leopard dace and slimy sculpins.

Columbia-Fraser Diversion

A diversion from the upper Columbia into the Fraser River system (Fig. 1) has been proposed as part of a plan to develop hydroelectric power on the Columbia, Thompson, and Fraser and on the diversion route itself. A high dam would be built at Mica Creek on the Big Bend of the Columbia; below this point water could be diverted alternately into Shuswap Lake on the Fraser system, or, during flood period on the Fraser, discharged down the Columbia (Department of Fisheries *et al.*, 1955). This would allow only a one-way transfer of fish.

No major alteration in fish distribution is likely to result from this diversion. Twenty-three species are now common to the Fraser and Columbia in British Columbia, and of the 20 further Fraser species all except the brassy minnow occur in the Columbia system in Washington. Twelve species are recorded from

the Columbia but not the Fraser. Six of these are introduced species (tench, northern black bullhead, yellow perch, largemouth and smallmouth bass, and pumpkinseed) which do not occur sufficiently far upstream to be involved in the diversion. Five native forms also have restricted ranges in the province remote from the proposed diversion (southern grayling and shorthead sculpins in the Flathead River, speckled dace in the Kettle River, Columbia sculpins in the Kettle and Similkameen rivers, and northern mountain-suckers in the Similkameen). One remaining species, the torrent sculpin, does occur in the Big Bend region of the Columbia and would probably spread into the Fraser. The pygmy whitefish, which is now known in the Fraser system only from Cluculz Lake and the Bowron Lake chain, is also abundant above the proposed diversion and would probably achieve wider distribution in the Fraser system.

Chilko Lake Diversion

This plan, like the tunnel already constructed from the Tweedsmuir Park chain of lakes into the Kemano River south of Kitimat (Fig. 1), involves the westward diversion of Fraser River water into a short coastal river (Water Powers, 1954). Chilko Lake, now tributary to the Fraser via Chilcotin River, would be dammed and its waters tunnelled into the Southgate or the Homathko rivers on Bute Inlet. Only one-way transfer of fish would be possible.

The Southgate and Homathko rivers are two of a series of short rivers on the west coast between Vancouver and Prince Rupert. Principal of these are the Squamish, Homathko, Klinaklini, Bella Coola and Dean Rivers (Fig. 1). Fish faunas of the area have not been thoroughly sampled, but available records are shown in the Appendix. At least 23 species probably occur in some or all of these drainages. Eighteen are anadromous or tolerant of salt water; the remainder have probably entered a few coastal systems by headwater capture from the Fraser. Because all of the 23 recorded species have been taken in both the Fraser and Skeena systems, diversions of Fraser waters such as that proposed at Chilko Lake are not likely to produce much alteration in fish distribution.

DISCUSSION

Not all of the proposed diversions discussed here are likely to be completed, but very probably some of them will. Those involving interchange between Pacific drainages are not liable to produce marked changes in fish distribution. If, however, waters are diverted across the continental divide, northern pike may be introduced, with possible serious economic consequences. Pike are known to be voracious fish-eaters, and they are known to be vectors of *Triaenophorus* tape-worm which can infect salmonid fishes as secondary hosts. In Alaska where pike and salmon occur together *Triaenophorus* does infect the latter. While it cannot be stated with certainty that pike, if introduced to Pacific drainages, *will* affect commercial and sport fishes, all evidence supports the distinct possibility that they *may* do so. Any effect which pike did have on Pacific salmon or trout would likely be harmful.

If a species occupies waters immediately upstream of a hydroelectric installation, there is every likelihood of that species eventually spreading downstream.

Although mortality of fish passing through a hydroelectric turbine is often high, all published studies have shown that mortality is not complete. A few individuals, particularly the very young, will survive passage through modern turbines and live to populate the waters below. To prevent passage of undesirable species, turbines might be modified specifically to kill fish entering them, although this unusual engineering problem would demand that even eggs and small larval fish be destroyed with certainty. If these stringent requirements could be met, it would in addition be necessary to ensure that water was never allowed to by-pass the turbines.

In the Atlin–Taku and Liard–Stikine schemes there is little doubt that the species which have been named would be present close to the diversion intakes. Except for the doubtful possibility of rendering these diversions impassable to all stages of live fish, some of these species would be virtually certain to find their way into Pacific watersheds. In the event that pike spread through the Stikine close to the headwaters of the Nass and Skeena, measures might conceivably be taken at obvious danger points to prevent their crossover into the more southerly drainages.

In the proposed Peace River development, the exact positioning of the dam in relation to the upstream limit of pike distribution would determine whether or not the reservoir contained pike. If pike were found to extend a short distance above the damsite, there might exist the practical possibility of poisoning the uppermost stretch of river at the time of closing the dam.

Certain records of fish distributions in the areas considered have been made only recently. Consequently, water diversions might produce distributional changes additional to those which can be foreseen on the basis of present knowledge.

The results, and even the occurrence, of some of the introductions discussed in this paper are uncertain. Nevertheless, any diversion of waters across the continental divide is virtually certain to bring about *some* changes in fish distribution. In economic terms the net result of these changes appears likely in most cases to be a loss rather than a gain. Such results should be considered in assessing the final effects of proposed hydroelectric developments.

ACKNOWLEDGMENTS

Valuable suggestions and criticisms of the manuscript have been received from W. A. Clemens, P. A. Larkin, R. G. McMynn, T. G. Northcote and E. H. Vernon. Information has also been kindly supplied by J. R. Adams, C. L. Anderson, R. M. Bailey, W. Kirkness, L. Margolis, D. E. McAllister, E. S. Marvich, R. R. Miller, R. R. Parker, J. W. Stokes and T. A. Walker. Specimens referred to were collected, under the auspices of the British Columbia Game Commission, with the assistance of J. W. Cartwright, E. Crichlow, E. J. Crossman, J. Dowsett, G. H. Geen, G. F. Hartman, H .W. Lorz, F. P. Maher, D. E. McAllister, M. A. Newman, W. G. Sparrow, E. H. Vernon and I. L. Withler. I wish particularly to acknowledge the assistance of S. B. Smith.

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APPENDIX: DISTRIBUTION RECORDS REFERRED TO IN TABLE I

Records from localities less than 5 miles from the sea have been omitted if the species recorded included only the following common coastal forms: Pacific salmon, cutthroat trout, steelhead trout, Dolly Varden, threespine stickleback or prickly sculpin.

Numbers preceded by "BC" refer to collections in the Institute of Fisheries, University of British Columbia. Species numbers are those assigned in Table I.

COLUMBIA RIVER SYSTEM IN BRITISH COLUMBIA

See Carl and Clemens (1953), Lindsey (1956b), and the following:

Thymallus arcticus tricolor (Cope), southern grayling—Flathead River near Montana border (BC56–107, BC56–494, BC56–577). (This form is probably identical with the extinct grayling of Michigan. Its relationship to the arctic grayling of northern British Columbia has yet to be determined.)

Pantosteus jordani Evermann, northern mountain-sucker—4 localities on Similkameen River drainage near Princeton (R. M. Bailey field collection No. B55–21, and BC55–398, BC56–89, BC56–374, BC56–488).

Rhinichthys osculus (Girard), speckled dace—2 localities on Kettle River (2 miles east of Rock Creek on B.C. Highway 3 (R. M. Bailey field collection No. B55–21), and 7 miles east of Rock Creek (BC56–492)).

Cottus hubbsi Bailey and Dimick, Columbia sculpin—11 localities on Similkameen River system in vicinity of Princeton (R. M. Bailey field collection No. B55–21, and BC54–193, BC54–338, BC56–89, BC56–129, BC56–132, BC56–338, BC56–374, BC56–488, BC56–504, BC56–505). Also Kettle River 12 miles east of Grand Forks (BC56–540).

Cottus sp., shorthead sculpin—3 localities in Flathead River near Montana border (BC55–276, BC55–278, BC56–577). (According to R. M. Bailey (pers. comm.) this is an undescribed form which is common in the Salmon River drainage of Idaho, and also occurs in northeastern Oregon and eastern Washington.)

Fraser River System

See Carl and Clemens (1953), Lindsey (1956b) and the following:

Acrocheilus alutaceum Agassiz and Pickering, chiselmouth—In addition to collections from the Okanagan River drainage, this species has been taken from 2 localities about 50 miles west of Quesnel, on the West Road River system tributary to the Fraser (BC56–569, BC56–611).

Homathko River System

Bluff Lake, expansion of Mosley Creek.
124° 43′ W., 51° 45′ N.
BC56–485: Species 41, 45, 55.

Sapeye Lake, tributary to Bluff Lake.
124° 43′ W., 51° 47′ N.
Game Commission records: Species 41, 55.

Tatlayoko Lake, expansion of Homathko River.
124° 24′ W., 51° 33′ N.
Game Commission records: Species 41, 45.

Klinaklini River System

One Eye Lake, expansion of Klinaklini River.
124° 54′ W., 51° 58′ N.
BC56–484: Species 35, 41, 45, 48, 50, 52?, 54, 55, 57.
Game Commission records: Species 35, 41, 45, 50, 53, 54, 57.

Bella Coola River System

Bella Coola River at Canoe Crossing about 25 miles east of Bella Coola.
126° 20′ W., 52° 26′ N.
BC56–480: Species 28, 34, 36, 45, 48, 50.

Snootshlee Creek, tributary to south side Bella Coola River, 6½ miles east of Bella Coola.
126° 36′ W., 52° 22′ N.
BC56–479: Species 31, 33, 34, 45.

Dean River System

Dean River 1½ miles from mouth.
126° 56′ W., 52° 49′ N.
BC55–265: Species 28.

Tanya Lake, head of Takia River.
126° 4′ W., 52° 47′ N.
J. W. Stokes (pers. comm.): Species 41, 45, 52, 57.

Sigutlat Lake, expansion of Iltasyuko River.
126° 13′ W., 52° 58′ N.
J. W. Stokes (pers. comm.): Species 41, 52, 53, 57.

Tusalko River about 20 miles west of Anahim Lake.
125° 41′ W., 52° 33′ N.
BC56–481: Species 57.
Nimpo Lake, expansion of Dean River.
125° 11′ W., 52° 29′ N.
BC56–483: Species 41, 45?, 52, 56, 57.
Dean River above Towdystan Lake.
125° 5′ W., 52° 16′ N.
BC56–482: Species 30, 41, 52, 54, 56, 57.

Skeena River System

Godfrey (1955) gives a bibliography on Skeena lakes. See also Lindsey (1956b) for record of *Coregonus coulteri*.

Nass River System

Lava Lake, head of Tseax River.
129° 0′ W., 55° 2′ N.
J. W. Stokes (pers. comm.): Species 50, 54, 57.
Sand Lake, tributary to Lava Lake.
128° 58′ W., 54° 58′ N.
BC56–620: Species 35, 53.
Meziadian Lake, tributary to Nass River.
129° 18′ W., 56° 4′ N.
BC55–221: Species 35, 41, 50, 53, 54, 55, 56, 57.
BC56–536: Species 41, 45, 50, 54, 55, 56, 57.
BC56–552: Species 41, 45, 50, 53.
Bowser Lake, expansion of Bowser River, tributary to Bell-Irving River.
129° 40′ W., 56° 26′ N.
BC56–537: Species 41, 45, 50.
Teigen Lake tributary via Teigen River to Bell-Irving River.
130° 8′ W., 56° 44′ N.
J. W. Stokes (pers. comm.): Species 36.
Damdochax Lake, tributary via Damdochax Creek to Nass River.
128° 6′ W., 56° 30′ N.
J. W. Stokes (pers. comm.): Species 30, 35, 36, 57.
Carl and Clemens (1953): Species 50.

Stikine River System

Shakes Creek, enters north side of Stikine River about 14 miles below Telegraph Creek.
131° 25′ W., 57° 47′ N.
W. Kirkness (pers. comm.): Species 36, 43, 45, 57.
Stikine River about 11 miles below Telegraph Creek.
131° 24′ W., 57° 49′ N.
BC56–499: Species 34, 36, 40, 41, 43, 50, 57.
Winter Creek, enters north side of Stikine River about 7 miles below Telegraph Creek.
131° 20′ W., 57° 52′ N.
BC56–498: Species 28, 30, 33, 34, 36, 40, 43, 45, 50, 57.
Stikine River at Telegraph Creek.
131° 10′ W., 57° 54′ N.
BC56–511: Species 34, 36, 40, 41, 46, 50.
Tuya Lake, head of Tuya River.
130° 33′ W., 59° 5′ N.
W. Kirkness (pers. comm.): Species 42, 43.

Tatsho Creek, flows southeast into Tanzilla River.
130° 9′ W., 58° 24′ N.
BC56–512: Species 40, 43, 57.
Cold Fish Lake, tributary to Spatsizi River.
128° 46′ W., 57° 40′ N.
BC54–485: Species 56.
T. A. Walker (pers. comm.): Species 43.

Taku River System

Taysen Lake chain, drains southeast into Nakina River.
132° 56′ W., 59° 16′ N.
W. Kirkness (pers. comm): Species 42, 44.
Tedideech Lake, drains north into Nahlin River.
131° 40′ W., 58° 46′ N.
W. Kirkness (pers. comm.): Species 43.
Taku River system.
R. R. Parker (pers. comm.): Species 29, 30, 31, 32, 33, 34, 35, 36, 37, 45, 50?, 57.

Alsek River System (not included in Table I)

Landlocked, in Yukon Territory.
Wynne-Edwards (1952): Species 35, 57.
Sockeye Lake, tributary to Kathleen Lakes.
137° 38′ W., 60° 30′ N.
Wynne-Edwards (1952): Species 47.
Dezadeash Lake, head of Dezadeash River, about 26 miles southeast of Haines Junction, Yukon Territory.
137° 0′ W., 60° 26′ N.
C. L. Anderson (pers. comm.): Species 43.
Wynne-Edwards (1952): Species 41.
Lakes in upper drainages.
E. S. Marvich (pers. comm.): Species 42, 43.
Alsek River system
R. R. Parker (pers. comm.): Species 36.
Wynne-Edwards (1952): Species 43, 61.
E. S. Marvich (pers. comm.): Species 29?, 33, 34, 35, 36, 37, 45, 57.

Yukon River System in British Columbia

See Clemens, Boughton and Rattenbury (1945), Withler (1956) and Lindsey (1956b).

Liard and Peace River Systems in British Columbia

See Lindsey (1956b).